Wright State University

CORE Scholar

Browse all Theses and Dissertations | Theses and Dissertations

2009

Risk-Sensitive Foraging Facilitates Species-Level Trophic Cascades Among Terrestrial Mammals: A Meta-Analysis

Bryan David Murray
Wright State University

Follow this and additional works at: https://corescholar.libraries.wright.edu/etd_all

 Part of the Biology Commons

Repository Citation

Murray, Bryan David, "Risk-Sensitive Foraging Facilitates Species-Level Trophic Cascades Among Terrestrial Mammals: A Meta-Analysis" (2009). *Browse all Theses and Dissertations*. 306.
https://corescholar.libraries.wright.edu/etd_all/306

This Thesis is brought to you for free and open access by the Theses and Dissertations at CORE Scholar. It has been accepted for inclusion in Browse all Theses and Dissertations by an authorized administrator of CORE Scholar. For more information, please contact library-corescholar@wright.edu.

RISK-SENSITIVE FORAGING FACILITATES SPECIES-LEVEL TROPHIC CASCADES AMONG TERRESTRIAL MAMMALS: A META-ANALYSIS

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

By

BRYAN DAVID MURRAY
B.S., Ohio Northern University, 2007

2009
Wright State University

Wright State University

School of Graduate Studies

August 18, 2009

I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY Bryan David Murray ENTITLED Risk-Sensitive Foraging Facilitates Species-Level Trophic Cascades Among Terrestrial Mammals: A Meta-analysis BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science

_____

Thomas P. Rooney, Ph.D.
Thesis Director

_____

David Goldstein, Ph.D.
Department Chair

Committee on Final Examination

_____

Thomas P. Rooney, Ph.D.

_____

Yvonne M. Vadeboncoeur, Ph.D.

_____

John O. Stireman III, Ph.D.

_____

Joseph F. Thomas, Jr., Ph.D.
Dean, School of Graduate Studies

ABSTRACT

Murray, Bryan David. M.S., Department of Biological Sciences, Wright State University, 2009. Risk-Sensitive Foraging Facilitates Species-Level Trophic Cascades Among Terrestrial Mammals: A Meta-Analysis.

The widespread removal of large carnivores from terrestrial ecosystems may be contributing to plant species loss and biotic homogenization through trophic cascades. A few plants not preferred by ungulates are increasing in abundance while the majority of preferred plants are in decline. A meta-analysis of recruitment gaps in browse-sensitive tree species demonstrated that failed recruitment coincided in time with carnivore loss. In all studies recruitment continued in nearby browsing refugia. A second meta-analysis revealed that the mechanism of mammalian herbivore-mediated trophic cascades contains a behavioral component. Foraging mammals exhibited higher giving-up densities (GUDs) when under higher predation risk. GUDs were highest in microhabitats perceived to be risky when predators were present, intermediate in safe microhabitats when predators were present, and lowest in safe and risky microhabitats in the absence of predators. Removing the landscape of fear may decrease spatial heterogeneity in plant communities, contributing to biotic homogenization.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

I would like to thank Tom Rooney for contributing a great deal of guidance, advice, and encouragement throughout every stage of this project. Thanks also to Robert Beschta and William Ripple for helpful advice on analyzing the recruitment gap data, as well as John Stireman and Yvonne Vadeboncoeur for their insightful comments on an earlier draft of this thesis. Special thanks go to my friends and family for their encouragement and support.

I. Trophic cascades, large carnivore loss, and the biodiversity crisis

The concept of trophic cascades is a recent development in ecology which has great potential for advancing our understanding of ecosystem function (Terborgh et al., in press). The most recent definitions of trophic cascades describe them as the top-down effects of carnivores on plants via herbivores (Pace et al. 1999, Schmitz et al. 2004). Discussion about trophic cascades began when Hairston et al. (1960) hypothesized that the world is green because carnivores regulate herbivore populations, allowing plants to be limited by resources rather than by herbivores (the green world hypothesis). Paine (1966) developed the "keystone species" concept that certain species exert a disproportionately large impact on the ecosystem relative to their abundance (see also Power et al. 1996). Estes and Palmisano (1974) demonstrated that the effects of a keystone species can "cascade" through the food chain to effect primary producers, a process which Robert Paine later named a "trophic cascade" (Paine 1980).

Trophic cascades can be either community-wide or species-specific (Polis 1999). The original definition of trophic cascades as described by the green world hypothesis (Hairston et al. 1960) and the exploitation ecosystems hypothesis (Oksanen et al. 1981) focused on the net effect of all species within a trophic level and ignored species-specific effects. Carpenter et al. (1985) used community-level cascades to demonstrate how the presence of predatory fish can decrease algal biomass in temperate freshwater lakes. The species involved in this trophic cascade are food generalists which demonstrates a community-level cascade. Trophic cascades have also been applied to species-specific

interactions within a community. Estes and Palmisano (1974) found that the presence of sea otters decreased the abundance of sea urchins allowing kelp forests to flourish. Other carnivores, herbivores, and plants are present in the system but the consumptive effect is limited to these specific species. In diverse and reticulate food webs community-wide changes in biomass may be rare whereas species-level cascades still occur (Polis 1999).

More recently discussion on trophic cascades has turned from whether they exist to where and at what magnitude (Schmitz et al. 2004). While evidence for trophic cascades accumulated quickly for aquatic ecosystems, many ecologists thought that they may be weaker in terrestrial ecosystems due to their reticulate structure. Impacts of top predators may attenuate quickly and never impact producers significantly (Polis and Strong 1996). However, a meta-analysis by Schmitz et al. (2000) demonstrated that species-level cascades should be common in terrestrial ecosystems. They found that 45 out of 60 studies reported significant indirect effects of carnivores on plants. The meta-analysis revealed that carnivore removal tends to positively affect herbivores and plant damage while negatively affecting plant biomass and reproductive output.

The meta-analysis by Schmitz et al. (2000) provided evidence for trophic cascades in terrestrial food webs but did not include any studies of vertebrate herbivores. Studies of trophic cascades involving vertebrates are rare and difficult to conduct due to methodological constraints and ethical concerns. A few researchers have taken advantage of serendipitous experiments to demonstrate trophic cascades involving vertebrate herbivores. McLaren and Peterson (1994) linked balsam fir (*Abies balsamea*) to the predator-prey dynamics of gray wolves (*Canis lupus*) and moose (*Alces alces*) in Isle Royale National Park where wolf and moose populations have been well-studied since

the 1950s. This long-term study has revealed that peaks in the wolf population are generally followed by troughs in the moose population. Balsam fir is an important winter browse species to moose. By analyzing tree rings McLaren and Peterson (1994) demonstrated that balsam fir grew more rapidly during high wolf/low moose density periods than when wolf density was low, linking wolves to balsam fir via moose. Terborgh et al. (2001) studied the densities of herbivores and plants on small, medium, and large islands in Lago Guri, a hydroelectric impoundment in Venezuela created in 1986. By 1993 herbivore densities were several times higher on small and medium islands compared to the mainland. Canopy trees failed to regenerate since the islands' creation whereas lianas, understory shrubs and bambusoid grasses increased in density. Hebblewhite et al. (2005) studied wolves and elk (*Cervus elaphus*) in Banff National Park. Wolves began recolonizing the Bow Valley in Banff in 1986, but tended to avoid areas where humans were common (Hebblewhite et al. 2005). Elk were more likely to be killed where wolf density was higher, therefore elk became more concentrated around human activity where wolves were more scarce. In the low-wolf/high-elk area near human activity aspen and willow were browsed more intensely, willow productivity was lower, and aspen recruitment was less (although not significantly). The presence of wolves also affected other species associated with willow such as beaver and songbirds.

The basic premise of a trophic cascade is that carnivores reduce herbivore biomass which leads to an increase in plant biomass. In order for this to occur, herbivore populations must be controlled by carnivores from the top-down rather than by plants from the bottom-up. The Schmitz et al. (2000) meta-analysis found that terrestrial carnivores generally have a direct negative effect on herbivore biomass. In the early 20th

century wildlife managers documented several deer population explosions following large carnivore removals (Leopold et al. 1947). Wolves are capable of regulating moose populations under certain wolf and moose population densities (Messier and Crete 1985, Ballard et al. 1987 Gasaway et al. 1992). Wolves are thought to have played a central role in the decimation of a wintering white-tailed deer (*Odocoileus virginianus*) population in a 3000 km^2 area of northeastern Minnesota during the 1960s (Mech and Karns 1977). Forest maturation, a series of seven severe winters, and the non-migratory behavior of the deer were thought to have made them more vulnerable to wolf predation (Mech and Karns 1977). As of 2004 deer had still failed to recolonize the area, therefore it seems that under certain conditions large carnivores can limit and potentially decimate cervid populations, although this example is the only documentation of wolves completely extirpating deer from an area (Nelson and Mech 2006).

While carnivores are capable of influencing herbivore populations, top-down control does not occur in all systems where both carnivores and herbivores are present. The top-down versus bottom-up dichotomy should rather be viewed as a continuum (Hunter and Price 1992). Wolves recolonized northern and central Wisconsin as well as upper Michigan during the 1980s and 1990s. Although wolf populations have stabilized deer population dynamics have not changed significantly (DelGiudice et al. 2009). The wolf's range in Wisconsin is inundated with human land use where wolves cannot establish territories. These areas may serve as refuges for deer to escape wolf predation similar to elk in Banff National Park (Hebblewhite et al. 2005). Prior to the Yellowstone wolf reintroduction critics claimed that wolves would greatly reduce the park's elk herd.

While the northern range elk herd declined after wolf reintroduction, the change has been primarily attributed to factors other than wolf predation (Smith et al. 2003).

The mechanism of a trophic cascade can be more complex than the consumptive effects of predators killing prey. Although wolf reintroduction in Yellowstone has not affected elk population size trophic cascades involving aspen (Ripple and Larsen 2000), cottonwoods (Beschta 2003, 2005) and willows (Beschta and Ripple 2007a, Beyer et al. 2007) have been reported. Trophic cascades can also be mediated through non-consumptive mechanisms such as prey behavior. Cognizant prey of various taxa have adapted anti-predator behaviors to increase their chances of survival in spite of predation risk. Strategies for reducing predation risk include avoidance of high-risk conditions, increased time spent vigilant, and grouping.

Prey can detect predation risk over space and time and attempt to avoid risky situations (Brown et al. 1999). High-risk conditions exist when predators are relatively successful at detecting and killing prey. They generally occur when prey cannot easily detect predators or when predators are present at high densities. In Yellowstone National Park elk altered their habitat use patterns in response to wolf predation risk (Fortin et al. 2005, Mao et al. 2005). Mao et al. (2005) analyzed elk radiotelemetry data before (1985-1990) and after (2000-2002) wolf reintroduction for changes in habitat selection. After wolf reintroduction elk summer habitat use shifted toward higher elevations, less open habitat, more burned forest, and steeper slopes where they were less likely to be killed by wolves. In winter elk selected more open habitats than after reintroduction, however, they did not spatially avoid wolves. During winter elk may rely more on grouping to reduce predation risk (Mao et al. 2005). Fortin et al. (2005) found that elk in high wolf use areas

of Yellowstone were more likely to move towards conifer forests than aspen stands compared to those in low wolf use areas.

Prey can also reduce predation risk by spending more time vigilant for predators, which increases the chances of early predator detection and prey escape. Impala (*Aepyceros melampus*) and wildebeest (*Connochaetes taurinus*) increased time spent scanning and the rate of scans following felid reintroduction in the Phinda Resource Reserve, South Africa, while no change in vigilance behavior was observed in a nearby area where felids remained absent (Hunter and Skinner 1998). Altendorf et al. (2001) found that mule deer (*Odocoileus hemionus*) spent more time vigilant and reduced foraging effort in areas of higher cougar (*Puma concolor*) predation risk. Although increased vigilance reduces predation risk, it also takes time away from fitness-improving activities such as feeding and reproduction (Lima and Dill 1990). Cow elk in Yellowstone have increased time spent vigilant since wolf reintroduction, which results in reduced time spent foraging (Laundré et al. 2001, Childress and Lung 2003, Wolff and Van Horn 2003, Winnie and Creel 2007).

The foraging effort of prey in relation to predation risk can be measured using giving-up densities (GUDs) (Brown 1988). GUD theory is based on the marginal value theorem (Charnov 1976). As a forager consumes a finite quantity of food, the value of each piece of food consumed declines with foraging effort. At a certain density of food the forager should "give up" and search for a new food patch because consuming one more piece of food would result in a net loss of overall fitness. GUD depends on the energetic cost of foraging, the cost of predation, and the missed opportunity cost of not doing something else. An increase in any of these costs will result in a forager leaving a

food patch at a higher GUD (Brown 1988). GUDs have been widely used to study foraging behavior of mammals (Verdolin 2006). Mule deer responded to levels of cougar predation risk by altering GUDs and habitat use at landscape and local scales (Altendorf et al. 2001). Nubian ibex have also been found to exhibit higher GUDs in riskier habitat types (Kotler et al. 1994). GUDs are a good estimate of perceived predation risk when energetic and missed opportunity costs are held relatively constant (Verdolin 2006).

Due to the anti-predator behaviors of prey, carnivores can initiate trophic cascades indirectly via fear in addition to the direct effect of killing prey (Brown et al. 1999). Herbivores living with the fear of predation will vary their foraging effort across the landscape in response to predation risk, creating grazing refugia in which plants experience reduced herbivory (Milchunas and Noy-Meir 2002). In Hebblewhite et al. (2005) the effect of wolf predation on aspen and willow was strongest in areas of high wolf density and low human use. A similar study in Zion National Park revealed higher mule deer densities, decreased plant, bird, and wildflower diversity, and increased stream erosion in an area avoided by cougar due to high human use (Ripple and Beschta 2006). The same impacts were not observed in a nearby area of low human use.

Vertebrate herbivores are known to affect plants in terrestrial ecosystems. Plant impacts of white-tailed deer in North America are well-documented. White-tailed deer tend to be selective feeders, focusing their foraging effort on finding and consuming the most nutritious and least defended plants (Smith 1991). When deer become overabundant they tend to overbrowse preferred species first allowing less preferred species to increase in abundance (Rooney and Dress 1997, Rooney et al. 2004, Rooney 2009, Thiemann et al. 2009). Rooney and Dress (1997) surveyed herbaceous plant abundance of the Heart's

Content Natural Area, an old-growth forest in the Allegheny National Forest of northwestern Pennsylvania and compared their results to a similar survey from the early 20th century. They were unable to find several plants from the original survey and others were found at low abundance. However, they found a greater abundance of graminoids and ferns which are not preferred by white-tailed deer. In a similar study conducted over a larger spatial scale, Rooney et al. (2004) resurveyed 62 upland forest plots from a 1950s Wisconsin plant inventory. Native species richness did not decline significantly on a regional scale, but on average declined 18.5% on a local (20 m^2) scale. In terms of community composition exotic species increased relative to native species at 80% of sites and habitat generalists increased while habitat specialists declined. Sites that gained species became more similar while those that lost species became more distinct due to the fact that nearly all species gained were invasive. Ironically, the sites with the most species loss were in state protected areas where human hunting is prohibited, therefore changes in plant communities likely occurred due to deer browsing. Rooney (2009) examined the species composition in 16-year exclosures compared to control plots in a high white-tailed deer density area. He found percent cover of woody plants, broadleaf herbs, and ferns to be much greater in exclosure than control plots. Alternatively, percent cover of sedges and graminoids, which are not preferred by white-tailed deer, was greater in control than exclosure plots indicating that intense deer herbivory is shifting plant community composition. Also, control plots were more similar to one another than exclosure plots indicating that deer herbivory is driving biotic homogenization of plant communities. Deer can also facilitate the invasion and persistence of exotic species. Chronic deer herbivory in Cades Cove, Great Smoky Mountains National Park prevented

native plants from outcompeting *Microstegium vimineum* during a drought (Webster et al. 2008). During a recent drought native plants temporarily gained an advantage over *Microstegium*. Inside deer exclosures this increase in abundance has been maintained at the expense of *Microstegium*, however, outside of the exclosures deer preference for the native species prevented them from maintaining increased abundance.

The concept of trophic cascades holds many applications for studying the impacts of humans on ecosystems (Terborgh et al., in press). One such pervasive impact is the removal of large carnivores. Much of the world's megafauna outside of Africa went extinct at the end of the Pleistocene approximately 10,000 years ago, a time which coincides with massive human dispersal (Martin 1973). The killing of large carnivores has accelerated over the last few centuries as the human population has exploded. Humans have effectively out-competed large carnivores across the globe by killing them directly, eliminating their food, and destroying their habitat. In natural systems competition sometimes results in the expansion of the more successful competitor at the expense of the less successful, which causes little change in the overall ecosystem if the two species are functionally equivalent. However, humans are not functionally equivalent to large carnivores (Berger 2005). As humans eliminate large carnivores we also eliminate the ecosystem functions that they perform as top carnivores. Some effects of carnivore removal such as increased herbivore density and subsequent plant damage are direct and easily observed. Several decades ago wildlife managers observed that deer irruptions tended to follow large carnivore removals (Leopold et al. 1947). Declines in vegetation were reported in areas of high cervid density within only a few years after these irruptions. A more recent review by Ripple et al. (in press) provided further support

that deer irruptions do not occur in the absence of large carnivore extirpation. Overabundant deer are common throughout temperate and boreal biomes and can cause profound changes in vegetation (Ripple et al., in press).

Other consequences of removing carnivores are indirect, unexpected, and not easily observed without careful study. Intense herbivory may suppress seedling and sapling recruitment of canopy trees. While the forest may appear to not change for centuries the adult trees will eventually die without replacement, converting the forest to unpalatable tree species or grassland. Reduced vegetation or altered plant species composition negatively affects other vertebrate and invertebrate animal species that depend on the vegetation for habitat or food (Berger et al. 2001, Hebblewhite et al. 2005, Ripple and Beschta 2006). In riparian areas, a loss of riparian trees can alter stream morphology by increasing bank erosion (Ripple and Beschta 2006, Wolf et al. 2007).

The removal of large carnivores could also contribute to the process of biotic homogenization. Biotic homogenization refers to the increase in genetic, taxonomic, and functional similarity between biotas over time (Olden and Rooney 2006). It is increasing on a global scale as human activities lead to species extinctions and introductions. Extinctions and introductions alone would not lead to homogenization, however, human activities tend to impact ecosystems in similar ways across the globe. Most invasive species are from the same few taxa and exhibit traits conducive to human-altered environments, long-distance dispersal, and rapid colonization. On the other hand extinction-prone species are also generally from similar taxa which tend to exhibit low reproductive rates, slow dispersal, habitat specificity, and poor adaptation to human-altered environments (McKinney and Lockwood 1999). Therefore human activities are

ultimately driving biotic homogenization by creating similar environments across the globe in which only a few taxa with a limited set of traits are able to survive.

Biotic homogenization appears even more insidious when considering the far-reaching impacts of the trophic cascades initiated when large carnivores are removed. I hypothesize that the loss of large carnivores is leading to biotic homogenization of plant communities by releasing ungulates from predation risk. Large carnivore loss should alter ungulate-plant interactions in two ways which allow the ungulate population to increase while preferred plant species decline. First, predation is no longer a mortality factor for ungulates, allowing individuals to generally live longer and produce more offspring. Second, ungulates do not need to be wary of predators, enabling them to forage wherever and whenever it is advantageous. Ungulate body condition should temporarily improve as more food becomes available, further increasing survival and reproduction rates. Preferred species are severely browsed by burgeoning ungulate populations allowing non-preferred species to increase in abundance.

If the hypothesis that carnivore removal negatively impacts browse-sensitive plant species is valid, then these plants should decline following the loss of carnivores. I tested this prediction by conducting a meta-analysis of tree age structures in western North American national parks where large predators were extirpated in the early 20th century. Secondly, I tested a set of hypotheses using meta-analysis to determine whether mammalian foragers spatially alter foraging effort based on predation risk. Data in support of these hypotheses would demonstrate that the loss of large carnivores throughout much of the world's temperate biomes has contributed to the biotic homogenization crisis.

II. Conducting a meta-analysis with log response ratio effect sizes

A meta-analysis is a quantitative synthesis of data from several existing studies in order to synthesize results and make between-study comparisons (Arnqvist and Wooster 1995, Hedges and Vevea 1998, Hedges et al. 1999). It allows the observation of patterns within or between studies that could not be detected by examining a single study in isolation. Meta-analysis involves computing an effect size between two treatments within each study, then computing a common effect size among all studies. This allows the researcher to determine the overall effect as well as identify studies that differ from the overall effect.

There are two general classes of meta-analysis techniques: fixed- and random-effects models (Hedges and Vevea 1998). Which class of models one chooses depends on the desired inference. Fixed-effects models estimate the mean effect size of a specific set of studies and should be used when conditional inference within the set is desired whereas random-effects models allow for unconditional inference that can be extended to studies outside of the set. The basic difference between the model classes is that fixed-effects models treat the effect sizes as fixed quantities whereas random-effects models treat them as random variables. In fixed-effects models the effect sizes are fixed, therefore the only source of error is in estimating effect sizes. In random-effects models the effect sizes are random variables distributed about a fixed mean. Random-effects models involve two sources of error: one in estimating effect sizes and another in estimating the mean of the effect size distribution (Hedges and Vevea 1998).

The need to conduct a meta-analysis arises when one is testing a hypothesis that involves combining and contrasting the results of several previous studies. Individual studies which appear to be similar may come to different conclusions, resulting in uncertainty and debate among researchers. A meta-analysis synthesizes results and helps identify factors influencing study outcome.

Conducting a meta-analysis involves forming a testable hypothesis, gathering appropriate data through a literature search, analyzing the data, and coming to a conclusion. Data is collected by conducting a literature search. Studies should meet a pre-determined set of selection criteria to be included in the analysis. These criteria are used to generate search terms for finding studies. Initial literature searches may result in an overwhelmingly large list of candidate studies, which could be reduced by using more specific search terms, but striking a balance between reducing the list while not excluding relevant studies can be challenging. Next, completely unrelated studies are eliminated by searching for which studies fit the general search criteria. Remaining studies are scrutinized very closely to make sure they contain sufficient data collected in an appropriate manner. Most meta-analytic methods require a minimum of the mean, standard error, and sample size of each treatment group. Data listed in tables can be easily extracted from studies, however, it is often necessary to estimate data based on figures.

The goal of the data analysis is to obtain the common effect size from data extracted from the studies and determine if it is significant. This is accomplished through a series of computations, including 1) effect sizes of each individual study, 2) fixed-effects weighted variance for each study, 3) fixed-effects weighted mean effect size, 4) an

estimate of between-studies variance, 5) random-effects weights for each study, 6) random-effects weighted mean effect size, and 7) the standard error of the weighted mean effect size (Hedges and Vevea 1998).

The type of effect size will depend on the nature of the data, but common measures of effect include the log response ratio, standardized mean difference, correlation coefficient, and odds ratio. I used the log-response ratio in all of my meta-analyses:

$$R_i = \log\left(\frac{\bar{X}_i^a}{\bar{X}_i^b}\right)$$

where $\bar{X}_i^a$ and $\bar{X}_i^b$ are the treatment means. The logarithm of the response ratio is advantageous over the response ratio because it is more linear (affected equally by changes in numerator or denominator) and has a normal distribution (Hedges et al. 1999). Because studies vary in precision, individual effect sizes must be weighted before computing the mean effect size, with more precise studies receiving greater weight. Based on Hedges and Vevea (1998), in the following meta-analyses I use the inverse variance weights:

$$w_i = \frac{1}{SE_i^2}$$

Using these weights the fixed-effects mean effect size is computed by:

$$\bar{R}_\cdot = \frac{\sum_{i=1}^{k} w_i R_i}{\sum_{i=1}^{k} w_i}$$

At this point in the analysis it is useful to determine whether significant between-studies variation exists in the data. If the goal of the study requires only conditional inference and

the effect sizes are homogeneous, then the analysis could potentially end here. The statistic Q can be used to test the homogeneity of effect sizes:

$$Q = \sum_{i=1}^{k} (w_i (R_i)^2 - \left(\frac{\left(\sum_{i=1}^{k} w_i R_i\right)^2}{\sum_{i=1}^{k} w_i}\right)$$

Q is essentially a ratio of between-study to within-study variance in effect sizes. It can used to test the null hypothesis that the between-studies variance $\hat{v}_\theta$ equals 0 (H_0: $\theta_1 = \theta_2 = \ldots = \theta_k$ where the θ_i are effect sizes). If Q is greater than the 100(1-α)% of the chi-squared distribution with k-1 degrees of freedom then the null hypothesis is rejected indicating that heterogeneity exists between effect sizes. If the null hypothesis is not rejected then the individual effect sizes are homogeneous (Hedges and Vevea 1998).

I chose to use a random-effects model because the ability to generalize my findings to additional situations is implicit in my goals. Between-study variance can be estimated by:

$$\hat{v}_\theta = \frac{Q - (k-1)}{\sum_{i=1}^{k} w_i - \frac{\sum_{i=1}^{k} w_i^2}{\sum_{i=1}^{k} w_i}}$$

The random-effects weights are computed by including the between-studies variance component in the inverse variance weights:

$$w_i^* = \frac{1}{SE_i^2 + \hat{v}_\theta}$$

Next the random-effects weighted mean effect size is computed by:

$$\bar{R}_\cdot^* = \frac{\sum_{i=1}^{k} w_i^* R_i}{\sum_{i=1}^{k} w_i^*}$$

The random-effects weights have been shown to be normally distributed about the true mean effect, therefore the weighted mean effect is an unbiased estimator of the true mean effect (Hedges et al. 1999). Because the weights are normally distributed one can determine if the weighted effect size is significant by testing the null hypothesis H_0: $\bar{R}_{\cdot}^{*} = 0$. This hypothesis is tested by constructing the 100(1-α)% confidence interval for $\bar{R}_{\cdot}^{*}$:

$$L = \bar{R}_{\cdot}^{*} - z_{\alpha/2} SE(\bar{R}_{\cdot}^{*}) \leq \mu \leq \bar{R}_{\cdot}^{*} + z_{\alpha/2} SE(\bar{R}_{\cdot}^{*})$$

$$\text{where } SE(\bar{R}_{\cdot}^{*}) = \sqrt{\frac{1}{\sum_{i=1}^{k} w_i^{*}}}$$

The null hypothesis is rejected if the confidence interval does not include zero, in which case one can conclude that the common effect of the treatment of interest is significant.

III. Meta-analysis reveals strong trophic cascades caused by large predator loss in western North America

INTRODUCTION

The occurrence of trophic cascades has become widely accepted in ecology. However, studies of trophic cascades have generally been limited to small spatiotemporal scales with small organisms conducive to manipulation. Ecological changes that occur over large spatiotemporal scales are difficult to observe and study. Chronically high deer browsing can lead to shifts in community composition away from browse-sensitive forest herbs and towards less palatable grasses, sedges, and ferns (Rooney and Waller 2003, Rooney et al. 2004, Rooney 2009). This transition has been noticed because it occurs on a time scale of years to decades, well within the human lifespan. Other impacts of chronically high deer browsing are more subtle because they are occurring over longer time scales which require long-term studies to detect. An increasing number of long-term studies have documented an impact of large carnivore loss on long-lived tree species which could play out over several decades.

Recruitment failure of browse-sensitive tree species such as quaking aspen (*Populus tremuloides*), cottonwoods (*Populus* spp.), willows (*Salix* spp.) and oaks (*Quercus* spp.) has been a widespread conservation issue in western North America since the early 20th century, mostly in national parks and other protected natural areas. One hypothesis for these recruitment gaps is that overbrowsing by abnormally high deer

populations, which tend to occur in protected areas, is preventing young trees from reaching the canopy (White et al. 2003). At low deer densities some young trees die from overbrowsing or trampling while a few survive to grow beyond the reach of deer. Under high and even moderate deer densities the proportion of browsing-related mortality increases substantially (White et al. 2003). In a natural ecosystem deer may occasionally halt recruitment over a time scale of years to decades over which long-lived species can survive. However, tree recruitment has been suppressed for nearly a century or more in much of the west, elevating long-term recruitment gaps to a major conservation concern. It may be difficult for long-lived species to recover from the current lapse in regeneration (Beschta 2003).

Variations on three general alternative hypotheses to deer overbrowsing have been proposed to explain recruitment gaps of different woody species in different areas, all of which maintain that deer are not overabundant. These include the natural regulation, disturbance regime change, and climate change hypotheses (White et al. 2003). According to natural regulation deer populations are regulated by density-dependent factors such as food and space. They are highly variable over time and directly impact the state of their preferred browse species, fluctuating between a low-density, abundant browse state and a high-density, depleted browse state. Woody browse has declined in the west over the 20th century because of a shift from the former state to the latter. Enough individuals survive in browsing refugia during periods of high deer density that species are rarely entirely extirpated (White et al. 2003). This hypothesis has greatly influenced park management policies in the United States since the 1970s (Kay 2001). It

implies that there is no deer problem and eventually deer densities will decline due to density-dependent processes.

Changes in disturbance regime can alter recruitment patterns of certain tree species including quaking aspen, cottonwoods, willows, and oaks. Aspen is a clonal species which rarely reproduces by seed, depending more on suckering and root sprouting to produce new stems. Fire facilitates the growth of new shoots by killing encroaching conifers and older aspen stems while enriching the soil with nutrients. Fire occurred frequently in the intermountain west prior to European settlement through natural causes and periodic burning of valley bottoms by Native Americans. A reduction in fire frequency due to intense fire suppression in the 20th century may have led to a decline in aspen recruitment frequency (White et al. 2003). Oaks may be adversely affected by fire regime change in a similar manner. Cottonwoods are riparian species whose successful reproduction has been linked to high peak flow years. Unlike aspen, cottonwood reproduce mostly from seed rather than suckers. They release more seeds in years of high peak flow and are capable of germinating in nutrient-poor soils. However, they are also highly shade-intolerant which prevents them from colonizing stream banks already occupied by plants. Reduced precipitation and human-altered hydrologic conditions may be reducing the habitats which cottonwoods need to regenerate (Beschta 2005). Willows are another group that may fail to regenerate without regular floods (Wolf et al. 2007). Hydrologic regime change in some areas has also led to a drop in the water table to the detriment of cottonwoods, willows, and other riparian plants (Beschta 2005, Ripple and Beschta 2006, Wolf et al. 2007, Beschta and Ripple 2008).

Climate change could also be responsible for recruitment gaps. The climate of the 20th century intermountain west was warmer and drier than that of the 19th century beginning with an extended drought in the 1930s. This drought correlates with the beginning of reduced recruitment in many areas (White et al. 2003, Beschta 2003, Beyer et al. 2007). Based on this observation some researchers have concluded that climate change is largely responsible for the recruitment gap. Much of the west may have previously been marginal habitat for certain woody species and an extended drought was enough halt regeneration (White et al. 2003).

Trees could also be failing to recruit due to altered trophic cascades by large carnivore removal. I hypothesized that the loss of carnivores throughout a large portion of western North America released deer from predation pressure (both real and perceived) increasing both the number and per capita impact of deer which in turn has caused recruitment gaps in preferred, browse-sensitive species (hereafter the "carnivore loss" hypothesis). I tested this hypothesis over a large spatial scale by conducting a meta-analysis of recruitment frequencies over time in 7 national parks. If carnivore loss is the primary cause of reduced recruitment then the beginning of the recruitment gap should correspond with the time of carnivore loss and should not affect trees in browsing refugia.

METHODS

To test the hypothesis that recruitment failure of browse-sensitive trees in western North America was ultimately caused by large carnivore loss, I conducted a meta-analysis of published studies on the age structure of these tree populations in relation to dates of carnivore loss. Long-lived tree species exhibit a Type III survivorship curve,

producing several seedlings of which only a few survive to reach the canopy, but those reaching the canopy can survive for several decades. Undisturbed tree populations that are successfully regenerating should be multi-aged with exponentially more younger than older trees. If carnivore loss halted recruitment then this age structure should have been disrupted beginning at the time that carnivores were removed, with more older than younger trees.

I conducted a formal literature search for studies with keywords "trophic cascade" of non-human mammals using BIOSIS. The initial list of 198 publications was narrowed down to those that 1) measured the age structure of a browse-sensitive tree population, 2) compared this age structure to that of a nearby grazing refuge to serve as a control, and 3) was conducted in a location with a well-documented history of large carnivore removal. I identified 8 publications with 10 individual studies that met these criteria. All of these studies were from national parks in the western United States and Canada and were of either wolf and elk or cougar and mule deer predator-prey systems. This limitation was due to the available literature rather than selection criteria. Data were extracted from figures using the program xyExtract Graph Digitizer (Silva 2008). Data subsequently obtained from the researchers indicated a data extraction error rate of less than 5% when using xyExtract.

To determine if recruitment declined at the time of carnivore loss I used the size of decadal age classes established before carnivore loss to predict the size of age classes that established after carnivore loss if trees were recruiting as expected. I estimated the expected age class sizes from carnivores absent decades using an exponential regression

model. I tested whether observed age class sizes from carnivores absent decades differed from expected using the log response ratio effect size:

$$R_i = \log\left(\frac{\bar{X}_i^O}{\bar{X}_i^E}\right)$$

where the $\bar{X}_i^O$ and $\bar{X}_i^E$ represent the observed and expected mean decadal age class sizes, respectively. All age class sizes were increased by 1 because some of them contained 0 trees. Data analysis was conducted using Microsoft Excel (Microsoft Office 2007).

There are three possible outcomes of the meta-analysis of which one would support the carnivore loss hypothesis while two would not. The carnivore loss hypothesis is supported if observed recruitment is much less than expected beginning at the time of carnivore loss, resulting in mean decadal effect sizes being significantly less than zero. Secondly, if the exponential models are not a good fit for the pre-carnivore loss age class data then recruitment declined significantly before carnivore loss and it is unlikely to be a primary driver. Thirdly, if observed recruitment after carnivore loss does not differ from expected then this would indicate that the recruitment gap began long after carnivores were lost.

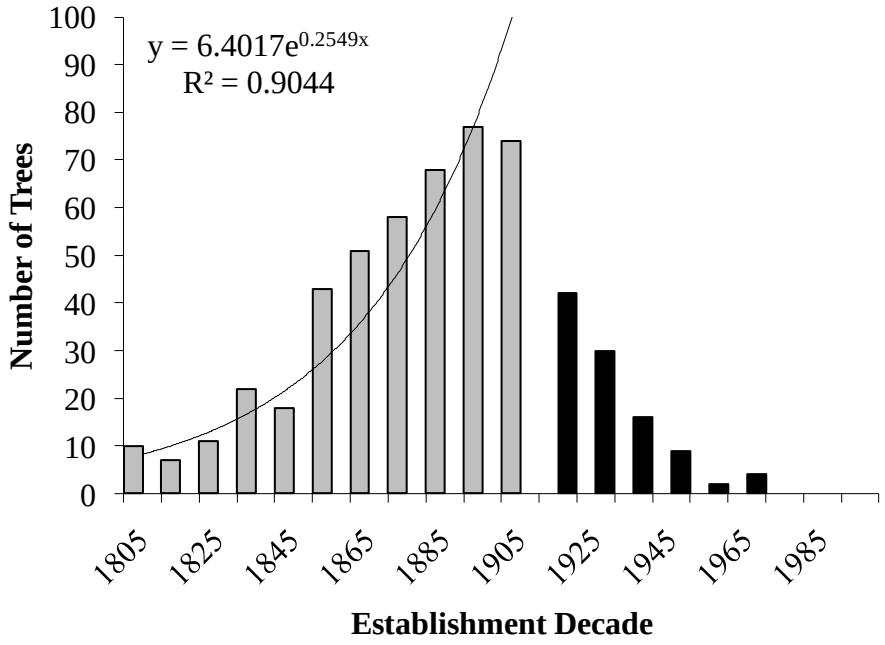
RESULTS

Age class sizes from before carnivore loss were as expected: recruitment occurred and age structures exhibited an exponential curve (Figures 1-10). The exponential models were a good fit for decadal age class sizes in all 10 studies with the minimum $R^2 = 0.58$ (Figures 1-10). Up until carnivore loss trees were recruiting as expected in both browsed and refugia plots (Figures 1-10).

The combined effect size of -1.791 ± 0.093 ($\bar{R}^{*}_{\cdot}$ ± 95% CI) indicates a 60-fold average difference between the observed and expected age class sizes during decades of carnivore absence (Figure 11). Observed age class size was significantly less than expected in all 10 studies. Individual effect sizes ranged from -1.20 for *Quercus kelloggii* in Yosemite National Park up to -2.73 (a 537-fold difference) for *Populus tremuloides* in Jasper National Park. Recruitment frequency began to decline within a few decades of carnivore loss in all 10 studies. Younger age classes were generally smaller than older age classes which is the opposite of what occurred prior to carnivore loss.

Tree stands in browsing refugia were multi-aged with exponentially more younger than older trees in all 10 studies. While all refugia plots exhibited this pattern only 3 contained enough trees that established before carnivore loss to fit a regression model. In these 3 plots neither the combined effect size (-0.105 ± 0.393) nor the individual effect sizes (Figure 12) differed from zero. Recruitment occurred in stands protected from deer browsing while it failed in those accessible to deer.

a.



b.

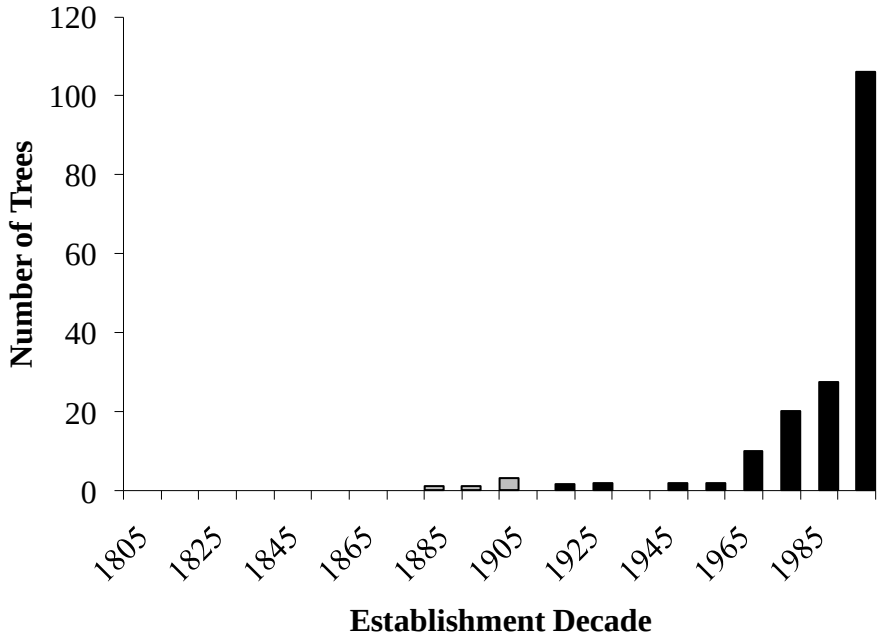


Figure 1: Observed (bars) and expected (regression line) age structures of black cottonwood (*Populus trichocarpa*) in a) plots with high elk densities within Olympic National Park, Washington, USA, and b) a plot on Quinault Indian Nation land with high human use and low elk density. Wolves were extirpated from the Olympic Peninsula by the early 1920s (Beschta and Ripple 2008).

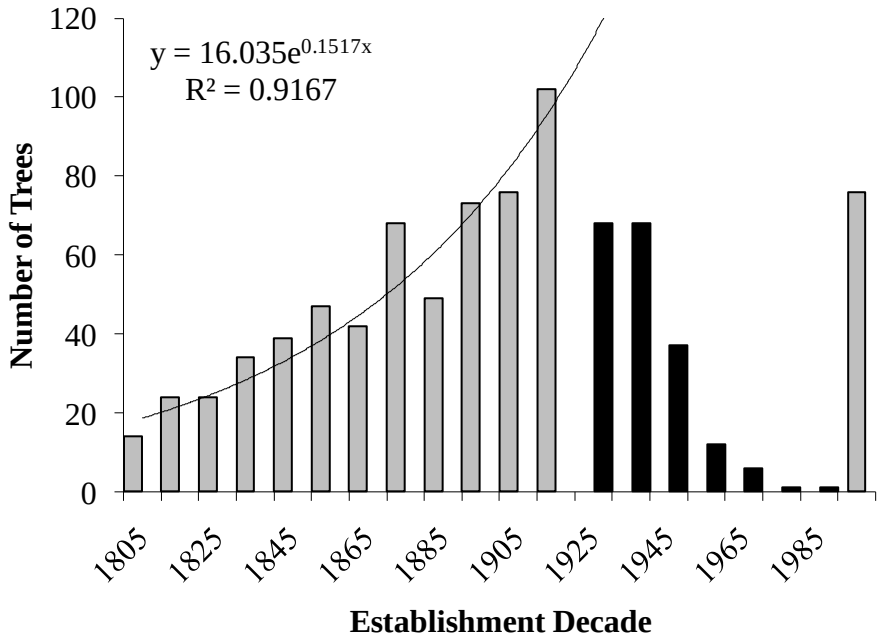


Figure 2: Observed (bars) and expected (regression line) age structures of black cottonwood (*Populus trichocarpa*) and narrowleaf cottonwood (*Populus angustifolia*) in plots exposed to elk browsing on the northern winter range of Yellowstone National Park, Wyoming and Montana, USA. Wolves were extirpated in the 1920s then reintroduced in 1995. The post-reintroduction age class size is shown but was not included in the regression model (Beschta 2005).

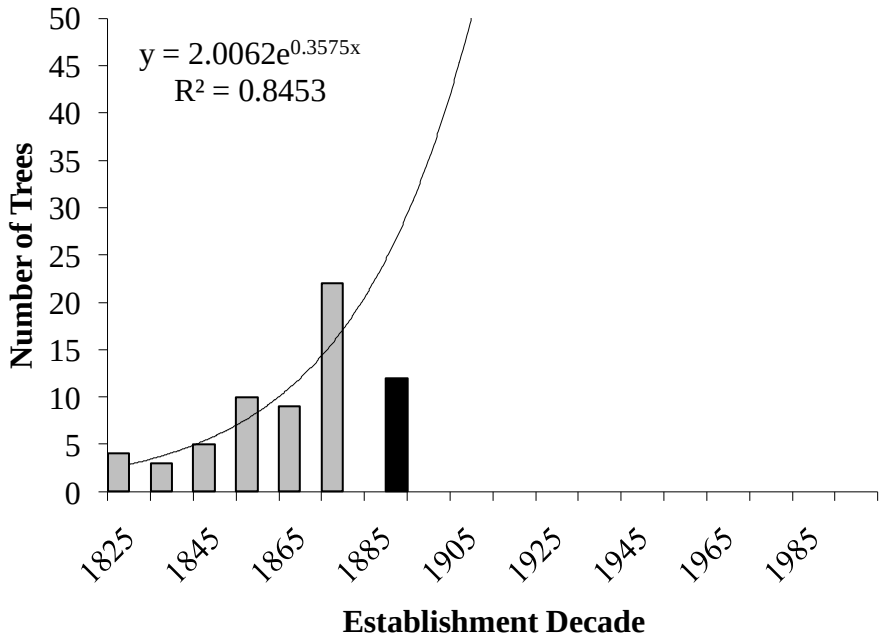
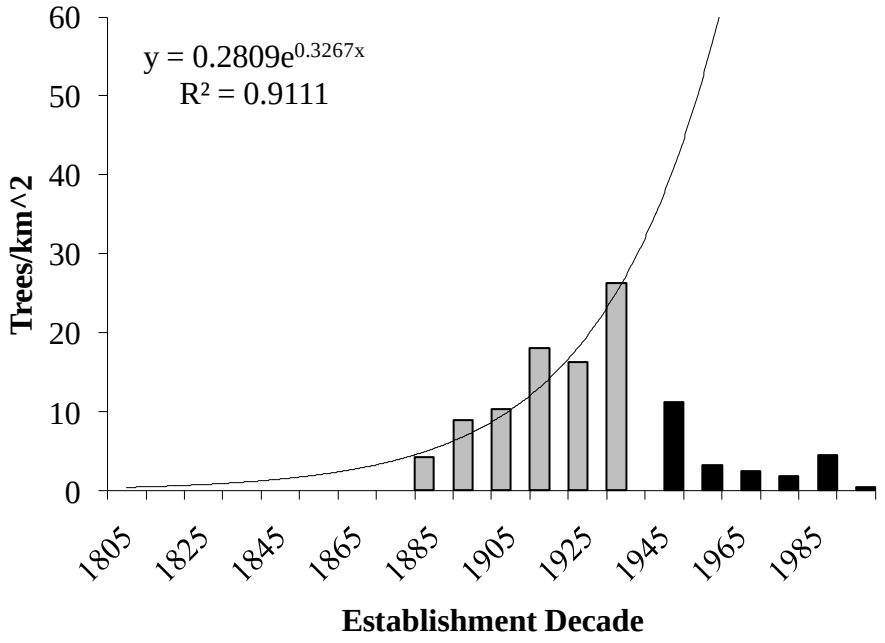


Figure 3: Observed (bars) and expected (regression line) age structures of plains cottonwood (*Populus deltoides*) and narrowleaf cottonwood (*Populus angustifolia*) in Wind Cave National Park, South Dakota, USA. Plots were exposed to browsing by wild ungulates including elk, mule deer, white-tailed deer, and pronghorn. Domestic livestock were also present from 1878 to 1946. Large carnivores including wolves and grizzly bears were greatly reduced by the 1880s (Ripple and Beschta 2007).

a.



b.

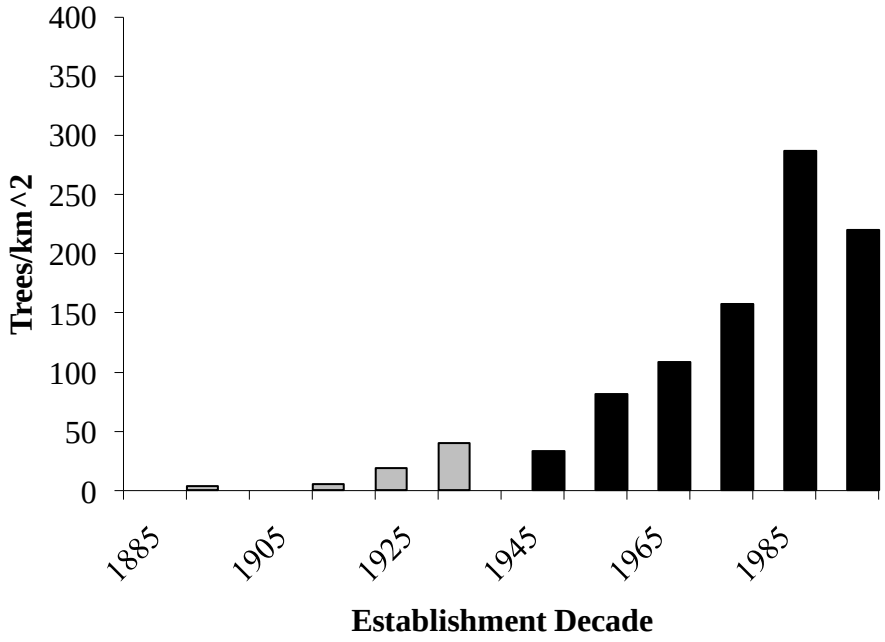


Figure 4: Observed (bars) and expected (regression line) age structures of Fremont cottonwood (*Populus fremontii*) in Zion National Park, Utah, USA, in a) Zion Canyon where cougar have been rare and mule deer density high since the 1930s and b) the North Creek drainage where cougar are currently common. Note the difference in scale between the y-axes (Ripple and Beschta 2006).

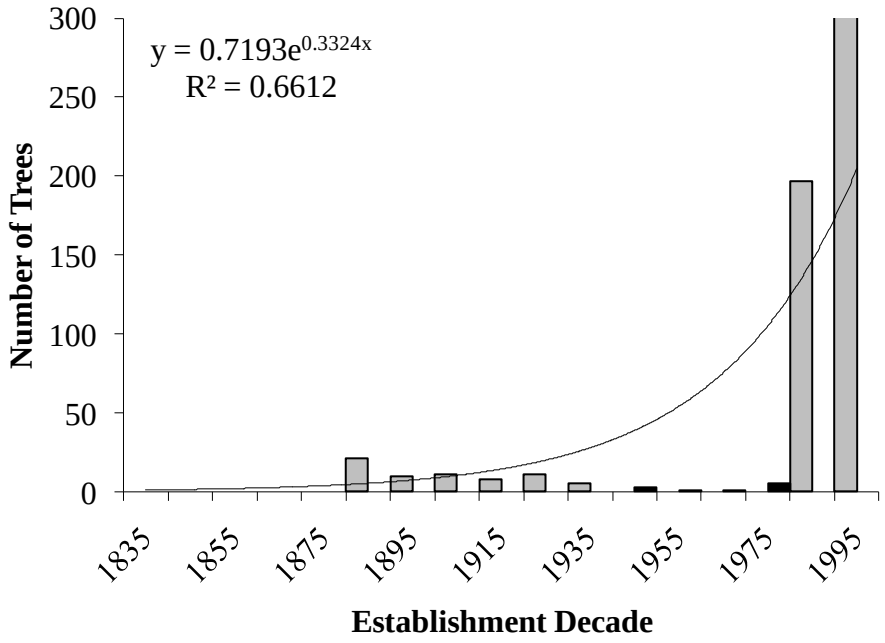


Figure 5: Observed (bars) and expected (regression line) age structures of quaking aspen (*Populus tremuloides*) in plots exposed to elk browsing in the Willow Creek area of Jasper National Park, Alberta, Canada, where wolves were absent from the 1930s to the 1980s (Beschta and Ripple 2007b).

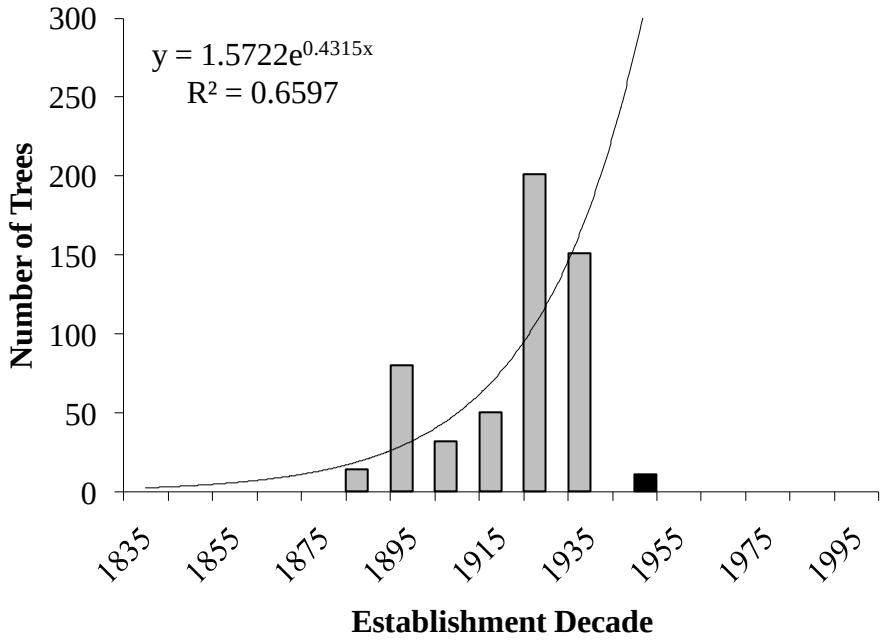


Figure 6: Observed (bars) and expected (regression line) age structures of quaking aspen (*Populus tremuloides*) in plots exposed to elk browsing in the Palisades area of Jasper National Park, Alberta, Canada, where wolves were extirpated by the 1940s (Beschta and Ripple 2007b).

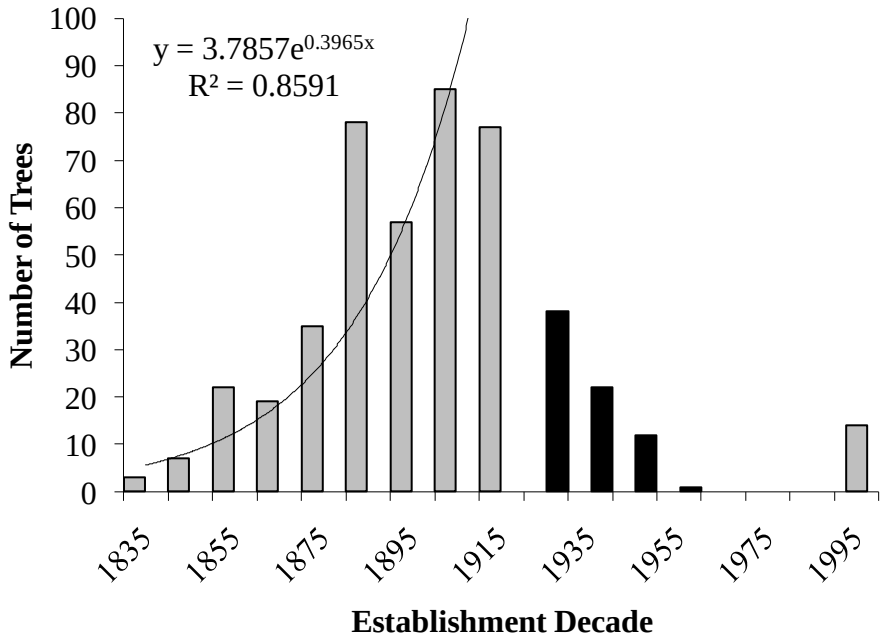


Figure 7: Observed (bars) and expected (regression line) age structures of quaking aspen (*Populus tremuloides*) in plots exposed to elk browsing on the Gallatin winter range of Yellowstone National Park, Wyoming and Montana, USA. Wolves were extirpated in the 1920s then reintroduced in 1995. The post-reintroduction age class size is shown but was not included in the regression model (Halofsky and Ripple 2008).

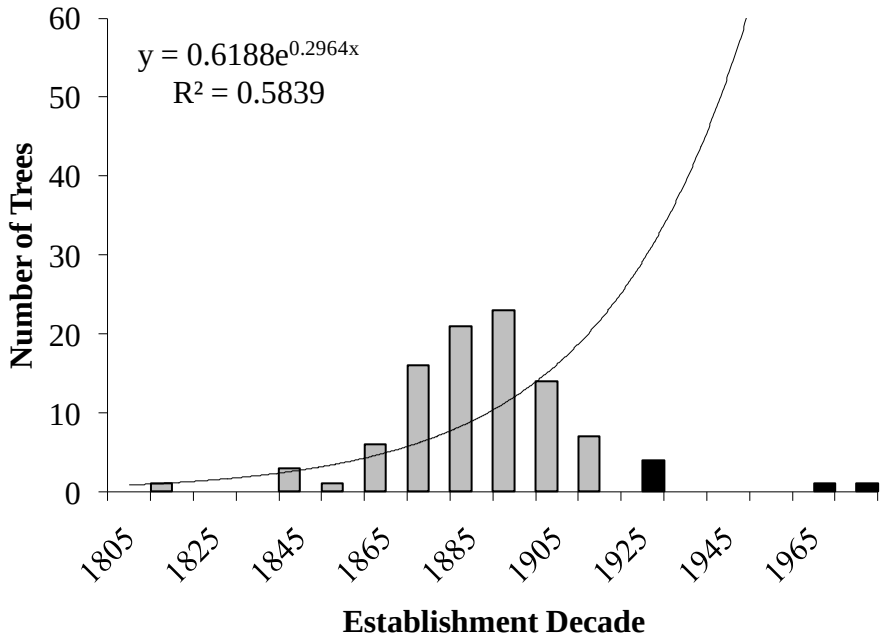


Figure 8. Observed (bars) and expected (regression line) age structures of quaking aspen (*Populus tremuloides*) in plots exposed to elk browsing on the northern winter range of Yellowstone National Park, Wyoming and Montana, USA, where wolves were extirpated in the 1920s (Ripple and Larsen 2000).

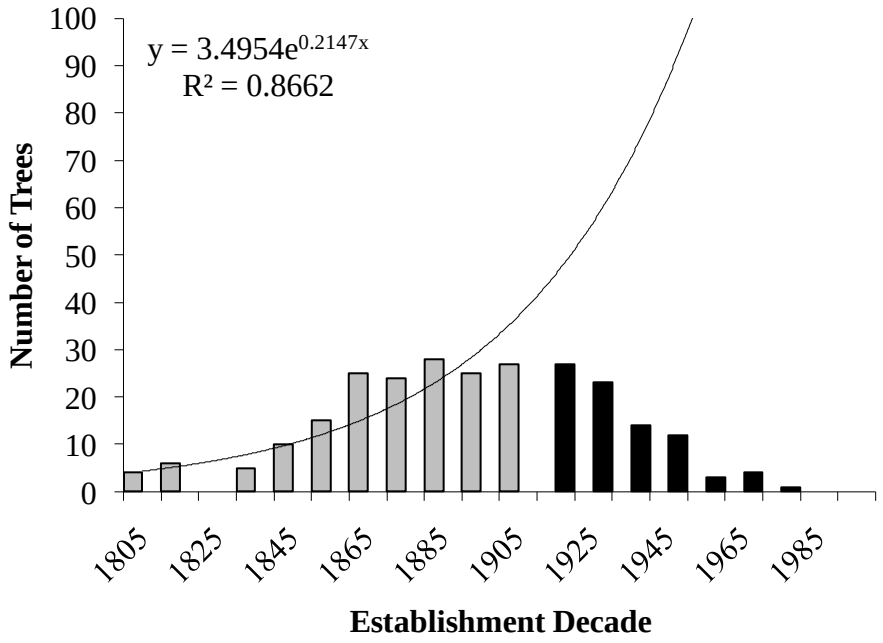
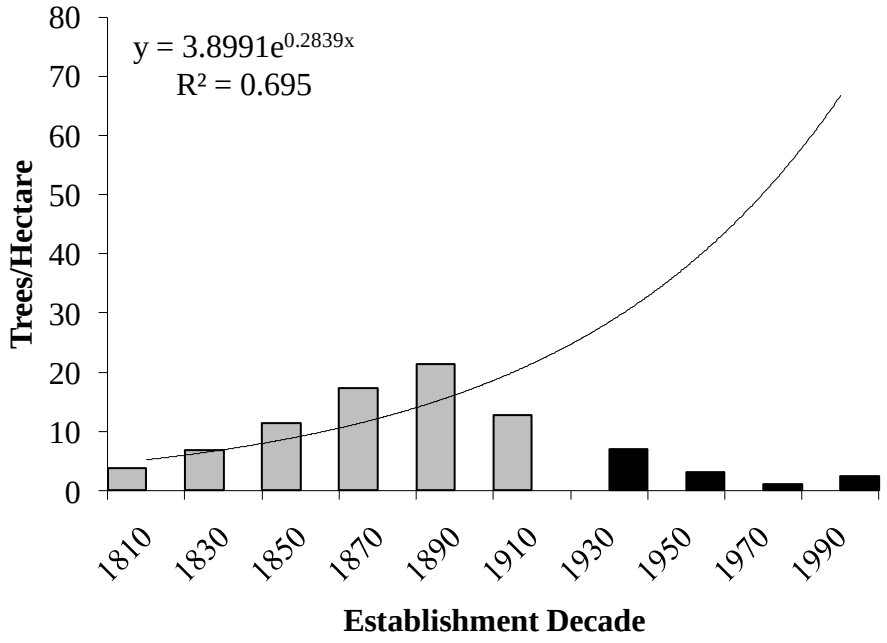


Figure 9: Observed (bars) and expected (regression line) age structures of bigleaf maple (*Acer macrophyllum*) in plots of high elk density in Olympic National Park, Washington, USA, where wolves were extirpated by the early 1920s (Beschta and Ripple 2008).

a.



b.

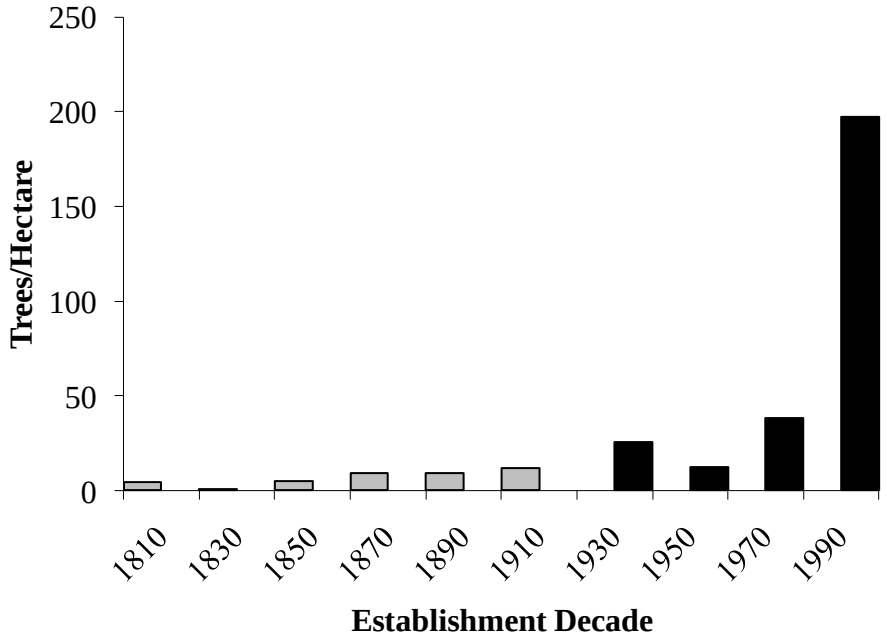


Figure 10: Observed (bars) and expected (regression line) age structures of black oak (*Quercus kelloggii*) in a) plots open to mule deer browsing and b) plots in browsing refugia in Yosemite National Park, California, USA. Cougar were extirpated from the park by 1920. Note the difference in scale between the y-axes (Ripple and Beschta 2008).

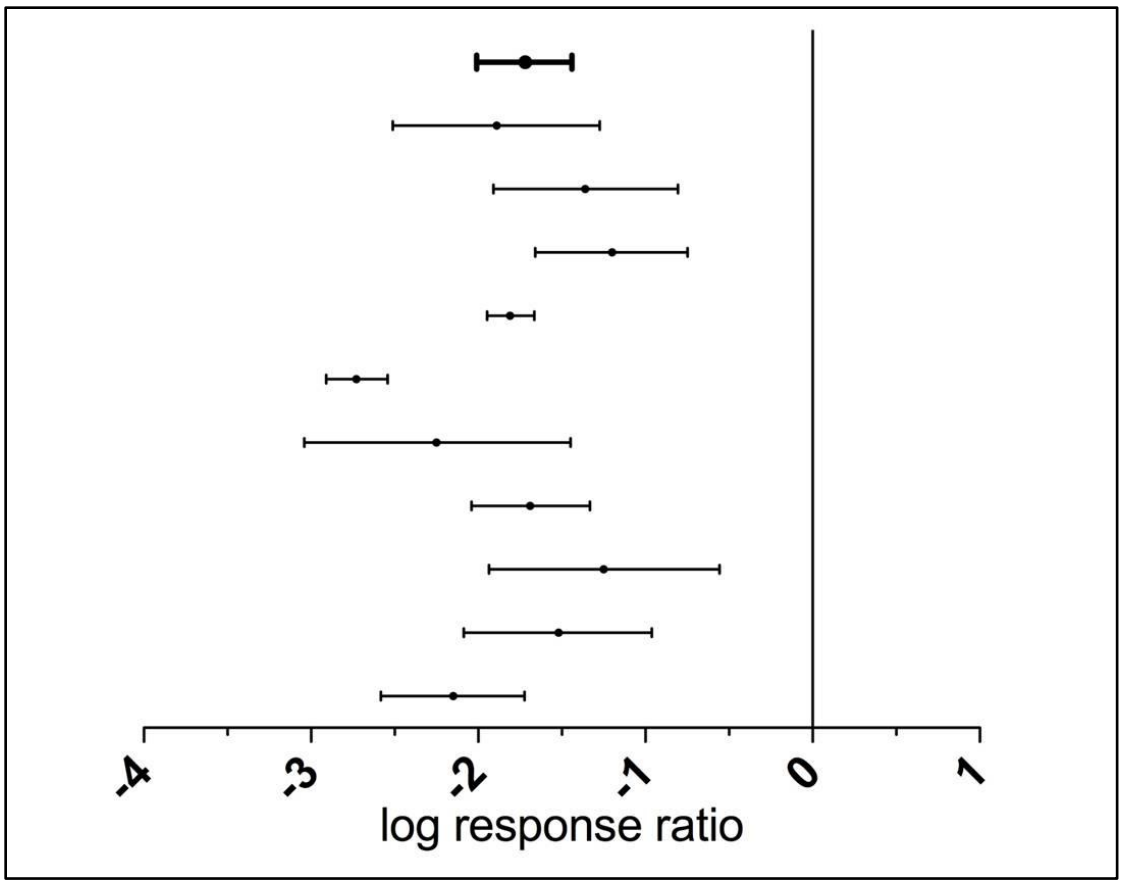
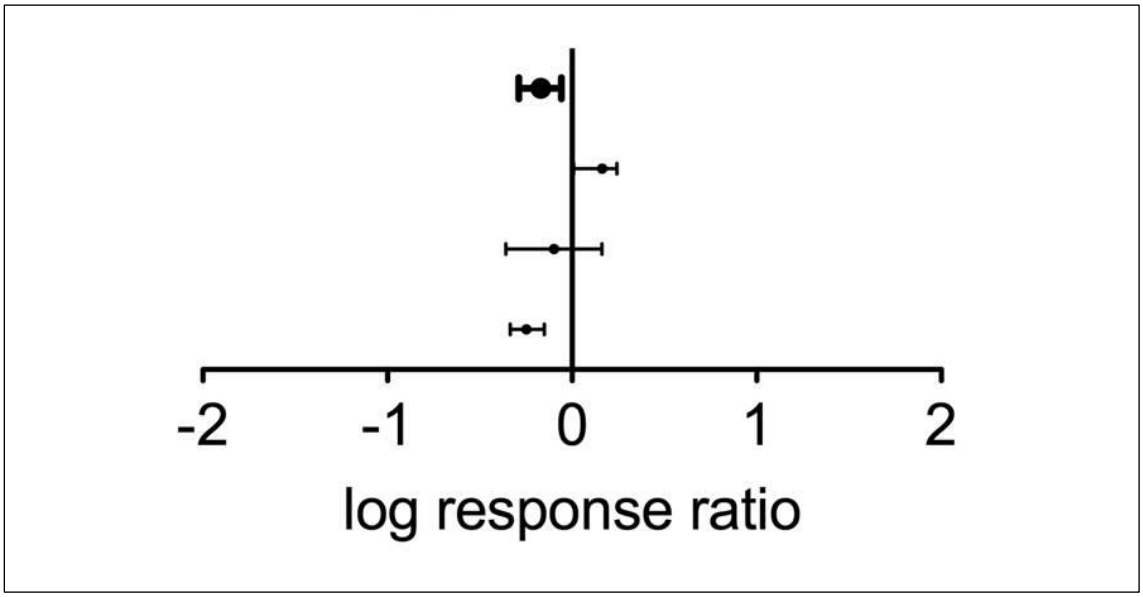


Figure 11: Mean log response ratio effect size (bold bar at top) and effect sizes of individual studies ± 95% confidence intervals from decades after carnivore loss all differed significantly from zero. Successful recruitment occurred much less than expected in the absence of carnivores.

a.



b.

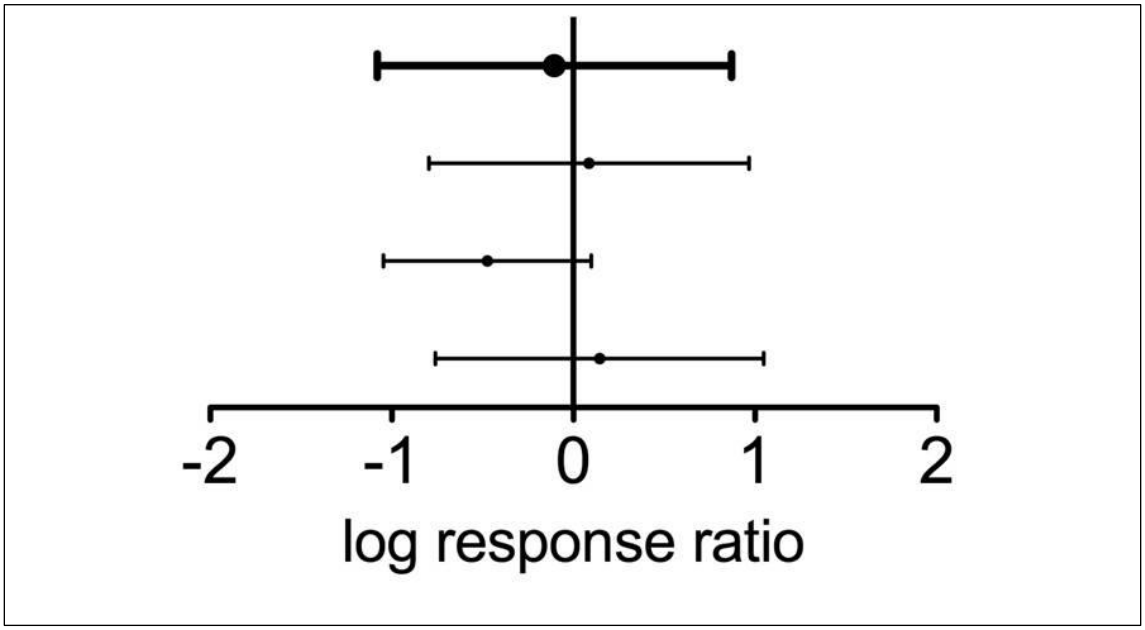


Figure 12: Mean effect size (bold bar at top) and effect sizes of individual studies ± 95% confidence intervals in browsing refugia from decades before (a) and after (b) carnivore loss.

DISCUSSION

The data supported the carnivore loss hypothesis that the loss of large carnivores can allow deer to suppress recruitment of browse-sensitive tree species. Recruitment began to decline immediately following carnivore loss in all 10 studies from 7 national parks located throughout western North America. Most stands exhibited a similar age structure: an exponentially increasing age class size, a leveling off or slight drop in the decades immediately before or after carnivore loss, then a sharp decline indicative of greatly reduced recruitment frequencies (Figures 1a, 2, 3, 4a, 5-9, and 10a). In each study recruitment occurred as expected within nearby browsing refugia (Figures 1b, 4b, and 10b) further supporting the carnivore loss hypothesis. Young stems in browsing refugia would have also failed to recruit if either climate change or reduced fire frequency were the primary cause. Additionally, recruitment has reinitiated in areas of high wolf predation risk to elk in parks where wolves have returned such as Yellowstone and Jasper (Figures 2, 5, and 7).

The removal of large carnivores by humans has provided a long-term experiment of terrestrial trophic cascades. Recruitment of young trees into the canopy occurred when carnivores were present but sharply declined after carnivore loss in all studies. In a few parks carnivores have returned and recruitment has resumed in certain areas. Each study alone provides compelling evidence for the existence of a large carnivore-induced trophic cascade. The meta-analysis demonstrates that each study is not idiosyncratic, but that trophic cascades may commonly occur in large carnivore-ungulate-plant food webs.

None of the alternative hypotheses alone explains the existence of recruitment gaps. Abnormally high deer densities may be part of the problem but do not tell the

whole story. Elk numbers were reduced by culling on the northern range of Yellowstone National Park until 1968 whereas the recruitment gap began when wolves were extirpated in the 1920s (Ripple and Larsen 2000, Beschta 2005). The natural regulation hypothesis does not logically explain the recruitment gaps. Browse-sensitive plant species are becoming reduced or disappearing from areas of high deer density (Rooney and Dress 1997, Rooney et al. 2004, Rooney 2009). If deer and plant communities were in a density-dependent equilibrium then extirpations should not occur. Either deer are unnaturally abundant or anthropogenic changes have indefinitely extended the high deer/low plant density state of the cycle. Certain species exhibiting recruitment gaps such as quaking aspen and cottonwoods also partially rely on disturbance events to regenerate. However, in Yellowstone National Park aspen failed to recruit in spite of the 1988 fires (Ripple and Larsen 2000, White et al. 2003) and cottonwoods did not recruit following several high flow events (Beschta 2005). The American west has experienced warmer and drier temperatures beginning with a major drought in the 1930s, which could have made many areas unsuitable for the growth of some species (White et al. 2003). However, young trees continued to recruit in refugia despite the altered climate. If climate change were the cause these trees would not be recruiting either. Climate change may interact with herbivory, making trees weaker and less able to tolerate natural herbivory levels. However, since trees would have still recruited under the same climate conditions in the absence of herbivory, climate change cannot be considered the primary cause.

While this meta-analysis is convincing, it could be built upon in future studies. The literature search could be repeated with search terms other than trophic cascade such

as top-down control, recruitment gap, and others. Tree stands in areas of continuous carnivore presence should be studied as controls, if they exist. Perhaps those studies have been done but were not published due to insignificant results. Ten studies is not many for a meta-analysis, sample size should be increased by replicating these methods in other areas, preferably outside of national parks. Unfortunately, few areas outside of the national parks have such a well-documented record of carnivore removal and are absent of other forms of human activity such as logging and development. Herbaceous taxa should receive attention as well, especially given the shorter time frame in which extirpation may occur.

The impact of carnivore loss on tree recruitment may be mediated by both lethal and nonlethal effects of carnivores on deer (Brown et al. 1999, Ripple and Beschta 2004). The lethal effects are that carnivores limit deer populations directly by killing deer, then there are fewer deer to browse trees. The second mechanism occurs because deer tend to avoid areas of high predation risk, creating behavioral browsing refugia where recruitment can occur. Upon carnivore loss these behavioral refugia may be eliminated, greatly reducing habitat suitable to tree growth. These data suggest that chronically high browsing pressure due to both increased deer densities and altered deer foraging behavior are significantly contributing to recruitment failure of browse-sensitive tree species.

IV. Meta-analysis of giving-up densities supports behavioral mechanism for trophic cascades

INTRODUCTION

Chapter 3 demonstrated that trophic cascades involving large terrestrial vertebrates can and do occur. However, few studies have demonstrated the mechanism leading from predators to herbivore habitat use to vegetation (but see Hebblewhite et al. 2005, Ripple and Beschta 2006). The nonlethal effects of predators on prey such as altered habitat use and reduced foraging rate should affect the composition and spatial distribution of plant communities. To reduce predation risk, herbivores forage more in safer than riskier areas such as elk in Yellowstone National Park (Fortin et al. 2005, Mao et al. 2005) and Banff National Park (Hebblewhite et al. 2005) and mule deer in Zion National Park (Ripple and Beschta 2006). This spatial pattern of habitat use structured by predation risk may cascade to the spatial distribution of vegetation. Areas perceived to be risky by herbivores can create biologically-maintained browsing refugia for the vegetation (Milchunas and Noy-Meir 2002). Many examples of such trait-mediated indirect interactions have been documented across several taxa (Werner and Peacor 2003). Browse-sensitive tree species such as aspen, cottonwoods, and willows have been regenerating in riparian areas of Yellowstone after wolf reintroduction. These species experienced multi-decadal recruitment gaps since the time of wolf extirpation (Ripple and Larsen 2000, Beschta 2005), but have resumed recruitment in areas of higher predation risk to elk such as riparian zones (Ripple and Beschta 2004). Browse damage to

aspen and willows was less in a high wolf-use area of the Bow Valley in Banff National Park (Hebblewhite et al. 2005). Recruitment gaps have also occurred in areas of low cougar use in Zion (Ripple and Beschta 2006) and Yosemite (Ripple and Beschta 2008) National Parks while recruitment continued in areas frequented by cougar.

Foraging effort can be quantitatively measured using giving-up densities (GUDs), the density of food remaining in a food patch when a forager gives up (Brown 1988). GUDs are measured by presenting foragers with food trays containing a known amount of food and inedible substrate. As each piece of food in the tray is consumed each subsequent piece becomes gradually more difficult to find until the energy gained from one more piece of food is less than the time and energy required to find it. At that point the forager should leave in search of another food patch. The density at which the forager leaves is the giving-up density (GUD) (Brown 1988). The GUD can be modeled by:

$$H = E + P + MOC$$

where H = harvest rate (rate of energy acquisition from food), E = energetic cost of foraging, P = predation cost of foraging, and MOC = missed opportunity cost of foraging (Brown 1988). The energetic cost of foraging is the energy expended while foraging and includes both metabolic costs and the costs associated with moving in search of food. The predation cost is energy lost in anti-predation activities. Missed-opportunity costs are those associated with feeding in the current patch rather than doing some other fitness-enhancing activity. A forager will continue foraging in a given patch as long as H is greater than the sum of E, P, and MOC. The optimal GUD occurs when H is equal to the sum of E, P, and MOC (Brown 1988).

GUD is a measure of a forager's perceived predation risk at a given place and time. Perceived predation risk is the forager's estimate of real predation risk. "Real predation risk" refers to the fact that there is a real density of predators, a real density of prey, and real variability across the landscape in the risk of a prey being captured and killed/consumed by a predator. "Perceived predation risk" refers to the ability of a cognizant prey to perceive its risk of being killed by a predator in a given place and time. Real and perceived predation risks are assumed to be imperfectly correlated due to the forager's limited ability to perceive its risk of predation (Brown et al. 1999).

To examine the effect of perceived predation risk on the foraging behavior of mammals, I conducted a meta-analysis of giving-up density studies. I hypothesized that GUDs would be directly related to perceived predation risk. A forager will choose to leave a patch that it perceives as riskier with a greater density of remaining food than the same forager would leave a safer patch, all else being equal.

I tested two further hypotheses to determine whether predator loss could lead to biotic homogenization of plant assemblages. I hypothesized that when predators are present at the habitat scale, strong differences in foraging effort should exist between perceivably safe and risky microhabitats. When predators are absent from the habitat this difference in foraging effort between microhabitats should be weaker or non-existent. Foragers should be able to perceive the lack of real predation risk when predators are absent and subsequently increase foraging effort (Brown et al. 1999). I also hypothesized that when predators are lost from an ecosystem foragers increase their foraging effort in formerly risky microhabitats to equal that of safe microhabitats because they can perceive that the entire habitat is effectively safe. To test these hypotheses I identified studies from

the previous meta-analysis which used a 2 x 2 factorial experimental design with perceived microhabitat type (risky and safe) and predation risk (present and absent) as the main effects (Table 1). I predicted that foraging effort should be lowest (GUDs highest) in risky microhabitats when predators are present, whereas the other three treatment combinations should exhibit similar levels of foraging effort (Table 1). If these hypotheses are supported it would indicate that biological browsing refugia exist only in risky areas in the presence of real predation risk. When predators are removed all habitats become safe to foragers and hostile to browse-sensitive plants.

Table 1. Perceived predation risk (as measured in GUDs) is expected to be significantly greater in risky microhabitats with predators present than in risky microhabitats without predators or safe habitats with or without predators.

		Microhabitat Type	
		Risky	**Safe**
Predators	**Present**	High	Low
	Absent	Low	Low

METHODS

I conducted a literature search in BIOSIS Previews which resulted in 195 potential papers. Search terms included "foraging and predation," "foraging and predation risk," "risk sensitive foraging," "GUDs," "foraging and predation risk trade-offs," "giving-up densities," or "giving-up densities and predation risk." This list was narrowed down to studies which 1) measured GUDs of a mammalian species, 2) experimentally isolated the cost of predation from energetic and missed opportunity costs, and 3) reported mean, standard error, and sample size of each GUD experiment.

The final list comprised 18 papers with 73 independent studies. Several papers contained more than 1 individual study by repeating an experiment on different species, varying the type of predation risk, or a combination of both. I considered these to be independent studies. Data were extracted from figures using the program xyExtract Graph Digitizer (Silva 2008) in studies which did not report data in the text.

All studies were included in a meta-analysis to test the first hypothesis. The effect of foraging in a patch under relatively lower perceived predation cost ("safe" patches) versus foraging in a patch under relatively greater perceived predation cost ("risky" patches) on GUDs was computed using the log response ratio:

$$R_i = \log\left(\frac{\bar{X}_i^R}{\bar{X}_i^S}\right)$$

as the effect size (Hedges et al. 1999), where R_i is the effect size, $\bar{X}_i^R$ is the mean GUD in the risky habitat, and $\bar{X}_i^S$ is the mean GUD in the safe habitat. I used a random-effects model with inverse variance weights to compute the average effect of studies. In studies of multiple levels of predation risk (i.e. riskiest, intermediate, and safest) I used the most extreme treatment levels (i.e. riskiest and safest) to compute the effect size. Data analysis was conducted in Microsoft Excel (Microsoft Office 2007).

The second set of hypotheses were tested by searching the previous list of 73 studies for those using a fully-crossed 2 x 2 factorial design with the treatments predators present versus absent (or low density) at the habitat scale and safe versus risky microhabitats. This search resulted in a list of 15 pairs of studies. I calculated effect size between safe and risky microhabitats using the same log response ratio and random-

effects model described preivously. The same group of studies was used to test the third hypothesis using the effect size:

$$R_i = \log\left(\frac{\bar{X}_i^P}{\bar{X}_i^A}\right)$$

where $\bar{X}_i^P$ is the mean GUD when predators are present and $\bar{X}_i^A$ is the mean GUD when predators are absent. With all effect sizes the mean GUD of the risky foraging condition is in the numerator while the mean GUD of the safe foraging condition is in the denominator so that a positive effect size supports the hypothesis that GUDs are higher under risky conditions.

RESULTS

The literature search returned 18 publications with 73 independent studies. On average, foragers abandoned risky food patches at higher GUDs than safe food patches according to the random-effects weighted mean effect size (0.071 ± 0.067; $\bar{R}_{\cdot}$ ± 95% CI). Of the 73 studies, 58 exhibited positive effect sizes which supported the hypothesis and 3 of those were significantly greater than zero (Table 2). Only one study had a significantly negative effect size (Table 2).

Fifteen of the 73 studies used to test the first hypothesis were amenable to testing the second and third hypotheses. When predators were present at the habitat scale, foragers abandoned risky microhabitats at higher GUDs than safe microhabitats (0.047 ± 0.022) (Figure 13). Two out of 15 individual studies exhibited a significantly positive effect size while 12 of the remaining effect sizes were positive but not significant (Table 3a). In the absence of predators, microhabitat type did not significantly affect foraging

effort (0.041 ± 0.063) (Figure 13). Of the 15 individual studies, 1 had a significantly positive effect size while 11 others were non-significantly positive (Table 3b).

The presence of predators had a significant effect on GUDs irrespective of microhabitat type (risky: 0.185 ± 0.119; safe: 0.121 ± 0.117) (Figure 14). In risky microhabitats 13 of 15 studies exhibited greater GUDs in the presence of predators with 5 being significant (Table 4a). In safe microhabitats GUDs were greater in the presence of predators in 11 of 15 individual studies of which 3 were significant (Table 4b). Only 1 study had a significantly negative effect size in both safe and risky microhabitats.

Table 2. Effect sizes (log response ratios) of individual studies from the GUD meta-analysis. Effect sizes that are significant and support the hypothesis are marked by "*" while those that are significant and do not support the hypothesis are marked by "+". Continued on page 47.

Publication	Species	R_i	-95% CI	+95% CI
Altendorf et al. 2001*	*Odocoileus hemionus*	0.26	0.04	0.48
Altendorf et al. 2001	*Odocoileus hemionus*	0.01	-0.31	0.33
Brown et al. 1992a	*Gerbillus allenbyi*	0.06	-0.36	0.49
Brown et al. 1992a	*Gerbillus allenbyi*	0.00	-0.27	0.28
Brown et al. 1992a	*Gerbillus allenbyi*	0.11	-0.10	0.31
Brown et al. 1992a	*Gerbillus allenbyi*	0.07	-0.05	0.19
Brown et al. 1992a	*Gerbillus allenbyi*	0.08	-0.04	0.20
Brown et al. 1992b	*Sciurus niger*	0.04	-0.82	0.91
Brown et al. 1992b	*Sciurus niger*	0.05	-1.43	1.53
Brown et al. 1992b	*Sciurus niger*	0.10	-1.12	1.32
Druce et al. 2006	*Procavia capensis*	0.03	-1.43	1.49
Guerra and Vickery 1998	*Tamiasciurus hudsonicus*	0.01	-0.94	0.96
Guerra and Vickery 1998	*Tamias striatus*	0.10	-1.02	1.21
Herman and Valone 2000	*Dipodomys merriami*	0.02	-0.12	0.16
Herman and Valone 2000	*Dipodomys merriami*	0.04	-0.10	0.18
Herman and Valone 2000	*Dipodomys merriami*	0.05	-0.02	0.12
Herman and Valone 2000*	*Dipodomys merriami*	0.10	0.02	0.19
Hochman and Kotler 2006	*Capra nubiana*	0.15	-4.57	4.86
Hochman and Kotler 2006	*Capra nubiana*	0.01	-12.25	12.28
Hochman and Kotler 2006	*Capra nubiana*	0.16	-12.76	13.08
Hochman and Kotler 2006	*Capra nubiana*	0.31	-12.42	13.03
Hochman and Kotler 2007	*Capra nubiana*	0.07	-6.99	7.13
Hochman and Kotler 2007	*Capra nubiana*	0.11	-6.54	6.75
Hochman and Kotler 2007	*Capra nubiana*	0.16	-7.19	7.50
Jacob and Brown 2000	*Microtus arvalis*	0.37	-0.26	1.00
Jacob and Brown 2000	*Microtus arvalis*	-0.29	-0.72	0.14
Kotler 1997	*Gerbillus allenbyi*	0.39	-0.02	0.80
Kotler 1997	*Gerbillus allenbyi*	0.19	-0.22	0.61
Kotler 1997	*Gerbillus pyramidum*	0.26	-1.13	1.65
Kotler 1997	*Gerbillus pyramidum*	0.11	-1.29	1.52
Kotler et al. 1998	*Pseudomys hermannsburgensis*	0.00	-0.63	0.63
Kotler et al. 1998	*Pseudomys hermannsburgensis*	0.00	-1.01	1.01
Kotler et al. 1998	*Pseudomys hermannsburgensis*	0.05	-2.28	2.39
Kotler et al. 1998	*Pseudomys hermannsburgensis*	0.01	-2.61	2.63
Kotler et al. 1998	*Pseudomys hermannsburgensis*	-0.02	-2.23	2.19
Kotler et al. 1998	*Pseudomys hermannsburgensis*	0.01	-2.54	2.56

Table 2: Continued from page 46.

Publication	Species	R_i	-95% CI	+95% CI
Kotler et al. 2004	*Gerbillus allenbyi*	0.11	-0.12	0.35
Kotler et al. 2004	*Gerbillus allenbyi*	0.06	-0.14	0.27
Mohr et al. 2003	*Mastomys natalensis*	0.01	-0.72	0.73
Mohr et al. 2003	*Mastomys natalensis*	0.13	-0.07	0.34
Mohr et al. 2003	*Mastomys natalensis*	0.16	-0.09	0.41
Mohr et al. 2003	*Mastomys natalensis*	0.04	-0.02	0.10
Mohr et al. 2003	*Mastomys natalensis*	0.06	-0.37	0.48
Mohr et al. 2003+	*Mastomys natalensis*	-0.19	-0.36	-0.03
Mohr et al. 2003*	*Mastomys natalensis*	0.23	0.08	0.38
Mohr et al. 2003	*Mastomys natalensis*	0.00	-0.09	0.09
Pickett et al. 2005	*Trichosurus vulpecula*	0.11	-5.77	5.99
Pickett et al. 2005	*Trichosurus vulpecula*	0.20	-4.36	4.76
Pickett et al. 2005	*Trichosurus vulpecula*	0.09	-3.49	3.67
Pickett et al. 2005	*Trichosurus vulpecula*	-0.28	-7.66	7.11
Pickett et al. 2005	*Trichosurus vulpecula*	0.00	-4.82	4.81
Pickett et al. 2005	*Trichosurus vulpecula*	0.17	-10.17	10.51
Pickett et al. 2005	*Trichosurus vulpecula*	0.07	-4.18	4.31
Pickett et al. 2005	*Trichosurus vulpecula*	-0.02	-6.53	6.48
Pusenius and Schmidt 2002	*Microtus pennsylvanicus*	-0.02	-0.11	0.07
Pusenius and Schmidt 2002	*Microtus pennsylvanicus*	0.22	-0.01	0.44
Schmidt 2000	*Sciurus niger*	0.12	-1.74	1.98
Schmidt 2000	*Sciurus niger*	0.22	-0.88	1.32
Schmidt 2000	*Sciurus niger*	0.25	-0.22	0.72
Tuen and Brown 1996	*Sciurus niger*	0.06	-0.45	0.57
Tuen and Brown 1996	*Sciurus niger*	0.03	-0.86	0.92
Tuen and Brown 1996	*Sciurus niger*	0.13	-1.55	1.81
Tuen and Brown 1996	*Sciurus niger*	0.02	-1.48	1.51
Tuen and Brown 1996	*Sciurus niger*	0.09	-2.41	2.58
Tuen and Brown 1996	*Sciurus niger*	0.16	-2.50	2.82
Yunger et al. 2002	*Phyllotus darwini*	0.07	-0.26	0.40
Yunger et al. 2002	*Phyllotus darwini*	-0.08	-0.47	0.31
Yunger et al. 2002	*Octodon degus*	0.00	-0.67	0.67
Yunger et al. 2002	*Octodon degus*	0.11	-1.36	1.58
Yunger et al. 2002	*Akodon olivaceous*	-0.04	-0.86	0.78
Yunger et al. 2002	*Akodon olivaceous*	-0.26	-1.53	1.01
Yunger et al. 2002	*Akodon olivaceous*	-0.01	-1.62	1.61
Yunger et al. 2002	*Akodon olivaceous*	-0.31	-2.02	1.39

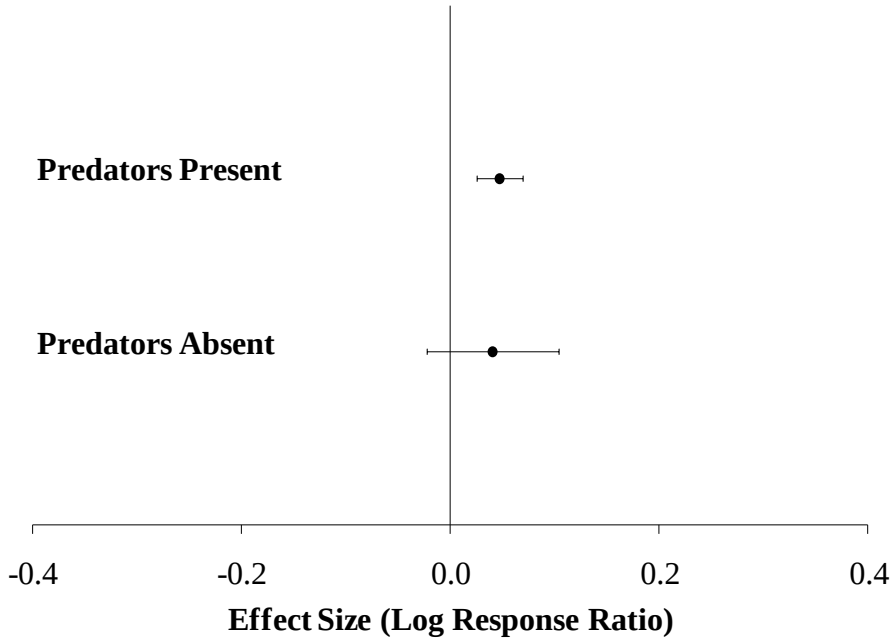


Figure 13. Random-effects weighted mean effect sizes $\overline{R}_{.}$ ± 95% confidence intervals of GUDs in risky compared to safe microhabitats in the presence and absence of real predation risk (k = 15 studies each). GUDs were higher in risky than safe microhabitats in the presence of predators but did not differ significantly when predators were absent, however, the effect of microhabitat on GUDs did not differ between predators present and absent treatments.

Table 3. Effect sizes and 95% confidence intervals from a) predators present and b) predators absent treatments. Significant effect sizes are marked by "*" if they support the hypothesis and "+" if they do not.

a.

Publication	Species	R_i	-95% CI	+95% CI
Altendorf et al. 2001*	*Odocoileus hemionus*	0.26	0.04	0.48
Brown et al. 1992a	*Gerbillus allenbyi*	0.06	-0.36	0.49
Herman and Valone 2000	*Dipodomys merriami*	0.04	-0.10	0.18
Herman and Valone 2000*	*Dipodomys merriami*	0.10	0.02	0.19
Jacob and Brown 2000	*Microtus arvalis*	0.37	-0.26	1.00
Kotler 1997	*Gerbillus allenbyi*	0.19	-0.22	0.61
Kotler 1997	*Gerbillus pyramidum*	0.11	-1.29	1.52
Kotler et al. 2004	*Gerbillus allenbyi*	0.06	-0.14	0.27
Mohr et al. 2003	*Mastomys natalensis*	0.01	-0.72	0.73
Mohr et al. 2003	*Mastomys natalensis*	0.13	-0.07	0.34
Mohr et al. 2003	*Mastomys natalensis*	0.16	-0.09	0.41
Mohr et al. 2003	*Mastomys natalensis*	0.04	-0.02	0.10
Pickett et al. 2005	*Trichosurus vulpecula*	0.11	-5.77	5.99
Pickett et al. 2005	*Trichosurus vulpecula*	-0.28	-7.66	7.11
Yunger et al. 2002	*Octodon degus*	0.11	-1.36	1.58

b.

Publication	Species	R_i	-95% CI	+95% CI
Altendorf et al. 2001	*Odocoileus hemionus*	0.01	-0.31	0.33
Brown et al. 1992a	*Gerbillus allenbyi*	0.08	-0.04	0.20
Herman and Valone 2000	*Dipodomys merriami*	0.02	-0.12	0.16
Herman and Valone 2000	*Dipodomys merriami*	0.05	-0.02	0.12
Jacob and Brown 2000	*Microtus arvalis*	-0.29	-0.72	0.14
Kotler 1997	*Gerbillus allenbyi*	0.39	-0.02	0.80
Kotler 1997	*Gerbillus pyramidum*	0.26	-1.13	1.65
Kotler et al. 2004	*Gerbillus allenbyi*	0.11	-0.12	0.35
Mohr et al. 2003	*Mastomys natalensis*	0.06	-0.37	0.48
Mohr et al. 2003*	*Mastomys natalensis*	-0.19	-0.36	-0.03
Mohr et al. 2003+	*Mastomys natalensis*	0.23	0.08	0.38
Mohr et al. 2003	*Mastomys natalensis*	0.00	-0.09	0.09
Pickett et al. 2005	*Trichosurus vulpecula*	0.20	-4.36	4.76
Pickett et al. 2005	*Trichosurus vulpecula*	-0.02	-6.53	6.48
Yunger et al. 2002	*Octodon degus*	0.00	-0.67	0.67

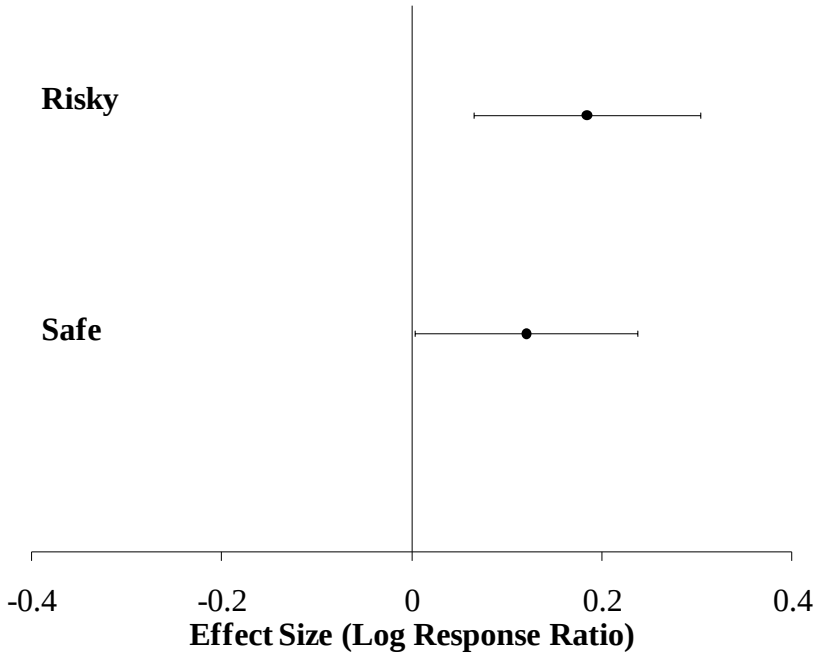


Figure 14. Random-effects weighted mean effect sizes $\overline{R}_{\cdot}$ ± 95% confidence intervals of GUDs in predators present compared to absent treatments in risky and safe microhabitat types (k = 15 studies each). The effect of predator presence significantly increased GUDs in both risky and safe microhabitats. Effect sizes did not differ between risky and safe microhabitats.

Table 4. Effect sizes and 95% confidence intervals from a) safe microhabitats and b) risky microhabitats. Significant effect sizes are marked by "*" if they support the hypothesis and "+" if they do not.

a.

Publication	Species	R_i	-95% CI	+95% CI
Altendorf et al. 2001	*Odocoileus hemionus*	0.04	-0.24	0.33
Brown et al. 1992a*	*Gerbillus allenbyi*	0.55	0.22	0.88
Herman and Valone 2000	*Dipodomys merriami*	0.03	-0.11	0.17
Herman and Valone 2000	*Dipodomys merriami*	0.03	-0.04	0.10
Jacob and Brown 2000*	*Microtus arvalis*	0.90	0.39	1.41
Kotler 1997	*Gerbillus allenbyi*	0.08	-0.11	0.28
Kotler 1997	*Gerbillus pyramidum*	0.28	-1.62	2.19
Kotler et al. 2004*	*Gerbillus allenbyi*	0.20	-0.05	0.45
Mohr et al. 2003	*Mastomys natalensis*	0.25	-0.22	0.72
Mohr et al. 2003*	*Mastomys natalensis*	0.41	0.26	0.56
Mohr et al. 2003*	*Mastomys natalensis*	0.27	0.07	0.46
Mohr et al. 2003+	*Mastomys natalensis*	-0.08	-0.14	-0.01
Pickett et al. 2005	*Trichosurus vulpecula*	0.27	-1.69	2.23
Pickett et al. 2005	*Trichosurus vulpecula*	-0.50	-7.62	6.63
Yunger et al. 2002	*Octodon degus*	0.37	-0.79	1.52

b.

Publication	Species	R_i	-95% CI	+95% CI
Altendorf et al. 2001	*Odocoileus hemionus*	-0.21	-0.48	0.06
Brown et al. 1992a*	*Gerbillus allenbyi*	0.56	0.28	0.85
Herman and Valone 2000	*Dipodomys merriami*	0.01	-0.13	0.15
Herman and Valone 2000	*Dipodomys merriami*	-0.02	-0.11	0.06
Jacob and Brown 2000	*Microtus arvalis*	0.24	-0.33	0.80
Kotler 1997	*Gerbillus allenbyi*	0.28	-0.27	0.83
Kotler 1997	*Gerbillus pyramidum*	0.43	-0.10	0.95
Kotler et al. 2004*	*Gerbillus allenbyi*	0.25	0.06	0.44
Mohr et al. 2003	*Mastomys natalensis*	0.30	-0.40	1.00
Mohr et al. 2003	*Mastomys natalensis*	0.08	-0.14	0.30
Mohr et al. 2003*	*Mastomys natalensis*	0.34	0.12	0.56
Mohr et al. 2003+	*Mastomys natalensis*	-0.11	-0.21	-0.02
Pickett et al. 2005	*Trichosurus vulpecula*	0.35	-6.83	7.53
Pickett et al. 2005	*Trichosurus vulpecula*	-0.24	-7.04	6.55
Yunger et al. 2002	*Octodon degus*	0.26	-0.87	1.39

DISCUSSION

The hypothesis that mammalian foragers reduce foraging effort when presented with higher predation risk was supported by the data. Foragers abandoned food patches at higher GUDs under risky compared to safe foraging conditions, therefore predation risk represents a real foraging cost to mammalian foragers. This phenomenon has been demonstrated in several studies and at least one previous meta-analysis (Verdolin 2006).

Interestingly, the random-effects weighted mean effect size was significantly greater than zero, but only 3 out of 73 studies exhibited a significantly positive effect. The mean effect size could be strongly influenced by a few precise studies since it was computed using inverse variance weights. Because inverse variance weights were used in computing the mean effect, the outcome of the meta-analysis could be dominated by a few highly precise studies, which may be the case here since the 3 significant studies are the 3rd, 10th, and 15th most precise studies out of 73. Also, only 6 of 35 studies greater than the median inverse variance are negative. Also, some of the included studies may have failed to find significance due to a low sample size. It could also be influenced by the scale at which predation risk affects behavior. The effect of predation risk on any one species' behavior in one location may not have a significant impact on behavior in that location, but the average effect over a larger scale may be significant. These are the types of effects that may not be revealed by individual studies by can be detected in a meta-analysis.

In contrast to the second hypothesis, foragers do not forage significantly less in risky microhabitats when predators are absent. The meta-analysis of GUDs in safe and risky microhabitats in the presence and absence of predators revealed that consumers

leave food patches at greater GUDs when predators are present but that there is no significant difference in GUDs between safe and risky microhabitats in the absence of predators.

Interestingly, effect sizes did not differ between locations with and without predators, however, the effect of habitat on GUDs was significant with predators present but not with predators absent (Figure 3). The variance of effect sizes was much higher in the absence than in the presence of predators, which could be an indication of variability in individual behavior. Even when predators are absent, many individuals may avoid risky areas due to an innate sense that the habitat type is not safe. Risk-prone individuals may venture into typically risky habitat and survive to feed there again. In contrast, when predators are present these risk-prone individuals either learn from experience to avoid these areas or die from predation. Therefore, an absence of predators may lead to more variability in forager behavior as exhibited by greater variance of GUD effect sizes.

The third hypothesis was only partially supported by the data. While effect sizes indicated higher GUDs in the presence of predators, this difference was observed in both risky and safe microhabitats. When predators are present, consumers in safe microhabitats are only relatively safe. While they may remain in safe microhabitats for longer time than risky microhabitats, they will ultimately leave at a higher GUD than they would in the complete absence of predation risk.

The meta-analyses demonstrate that GUDs are highest when predators are present than when they are absent in both risky and safe microhabitat types. Also, GUDs are greater in risky than safe microhabitat types in the presence of predators but not in their absence. On average, the lowest foraging effort should be found in risky microhabitats in

the presence of predators, which is what was expected. Intermediate foraging efforts are expected in safe microhabitats when predators are present. The lowest GUDs and highest foraging efforts should occur in both risky and safe microhabitats when predators are absent (Table 5a).

The results indicate that a population increase of foragers could occur when predation risk is removed. While the average effect size was not different between predators present and absent treatments, there was more variation in effect sizes when predators were absent. Safe areas support larger forager populations with greater competition than risky areas. Less competitive individuals in this environment are often faced with a trade-off between remaining and potentially starving or dispersing to a less favorable habitat (Lidicker and Stenseth 1992). When predators are present, these individuals disperse to risky areas and are eaten by predators, both feeding the predators and decreasing the surplus population of consumers. When predators are removed these less fit individuals are able to find suitable habitat without predation risk or intense competition. Eventually formerly risky areas become saturated with consumers and less fit individuals have no less competitive environment to disperse. Browsing pressure should eventually increase across the landscape. Future studies should measure changes in GUDs over time to study this potential effect.

In the absence of predation risk foragers devote more effort to foraging in both risky and safe areas. Greater foraging effort was observed in both safe and risky areas without predators. Large terrestrial carnivores have been removed from much of the earth's temperature biomes. Before carnivore removal browsing pressure was spatially structured as described above, with low browsing pressure in high-risk areas and

intermediate browsing pressure in low-risk areas (Figure 5b). Upon carnivore removal herbivores dispersed across the landscape without concern for predation risk. Instead of herbivores existing in pockets of high and low densities, densities became universally high on a large scale. Browsing pressure reached unprecedented levels of which most plants lack adaptations to withstand.

Table 5: a) Impact of predation risk on GUDs and b) predicted impact of predation risk on browsing pressure.

a.

		Microhabitat Type	
		Risky	**Safe**
Predators	**Present**	High	Intermediate
	Absent	Low	Low

b.

		Microhabitat Type	
		Risky	**Safe**
Predators	**Present**	Low	Intermediate
	Absent	High	High

V. Conclusions

Strong trophic cascades involving vertebrate herbivores can exist in terrestrial ecosystems. Recruitment of browse-sensitive tree species rapidly declined immediately following large carnivore extirpation in western North America (Chapter 3). The results of this meta-analysis can be generalized to other carnivore-herbivore-plant associations beyond the national parks of western North America. Given that large carnivores have been extirpated, driven extinct, or greatly reduced throughout the world in terrestrial, aquatic, and marine ecosystems this information could be highly useful to conservation biologists.

The presence of predators increases biotic heterogeneity at the landscape scale by creating a landscape of fear (sensu Brown et al. 1999). The foraging effort of a mammal decreases as perceived predation risk increases (Chapter 4). When predators are present across the landscape foragers respond by spending less time in risky habitat types and being more vigilant for predators if they do venture into a risky area. As a result, landscape-wide foraging effort is relatively moderate, while foraging effort in particularly risky habitat and microhabitat types is very low. If predators are removed from this system foragers benefit by expanding their spatial habitat use and spending more time feeding and less time vigilant. Foraging effort becomes uniformly high across the landscape.

Deer tend to forage selectively, focusing on the most nutritious and palatable plant species (Smith 1991). Deer populations irrupted in the early 20th century, shortly

after widespread carnivore extirpation and state regulation of deer hunting (Leopold et al. 1947, Rooney and Waller 2003). They are currently abnormally high in many areas of the United States (Rooney and Waller 2003). In areas of high abundance they are shifting plant community composition towards less palatable species while preferred species are in decline (Rooney and Dress 1997, Rooney and Waller 2003, Rooney et al. 2004, Rooney 2009).

Prior to carnivore extirpation, the response of deer to predation risk maintained browsing refugia for which certain highly nutritious and palatable plant species were able to thrive even at moderate deer densities. Plant diversity was increased across the landscape due predation risk-maintained heterogeneity in plant community composition. maintains browsing refugia in which palatable plant species can persist even when herbivores are common across the entire landscape. In the absence of carnivores deer have been able to relax their wariness for predators and increase foraging effort on plants, thereby contributing to biotic homogenization.

Large carnivore loss contributes to the biotic homogenization of plant assemblages through 3 main mechanisms. These include 1) a numerical increase in herbivores, 2) the elimination of biological browsing refugia, and 3) increased per capita browsing impact of each herbivore. The first mechanism is caused by reduced direct mortality to predators. The second and third mechanisms are linked to the absence of real predation risk which allows herbivores to forage in formerly risky areas while increasing foraging effort and decreasing selectivity. Plans to restore plant biodiversity to ecosystems degraded by chronic herbivory should consider each of these mechanisms to be fully successful. If deer reduction alone is used, then densities will have to reach

extremely low levels to restore palatable species because deer will seek out these preferred species. If herbivore densities become too low then homogenization may occur through the dominance of palatable, more competitive species. If carnivores are restored they may not be capable of reducing abnormally abundant deer densities without some culling of the deer herd, as in Wisconsin where deer population dynamics do not seem to have been significantly affected by wolf recolonization (DelGiudice et al. 2009). Creating physical browsing refugia is one alternative to culling deer and restoring predators. While it would be better than nothing, physical refugias entirely exclude all deer herbivory and do not shift over time. Biological browsing refugia are fuzzy boundaries that allow moderate levels of browsing and shift in space over time (Milchunas and Noy-Meir 2002), therefore physical refugia may not functionally replace biological refugia.

This study does provide evidence for the existence of large mammal terrestrial trophic cascades and helps describe the mechanisms. Schmitz et al. (2000) and other meta-analyses have demonstrated that species-level trophic cascades can occur in terrestrial ecosystems of invertebrate herbivores. The meta-analysis of Chapter 3 demonstrates that vertebrate herbivores can also be involved in trophic cascades. A meta-analysis that included both invertebrate and vertebrate herbivores would be useful, but is not practical with the current data. Only a few studies have explicitly linked carnivore presence, risk-sensitive foraging behavior of deer, and vegetation decline in the same ecosystem (but see Hebblewhite et al. 2005). Such a study is not easily accomplished when large vertebrate animals and long-lived tree species are involved.

Large carnivore loss is an important driver of biotic homogenization. The first and most obvious loss of diversity is the carnivore itself. Deer increase in density and spread

out across the landscape immediately following carnivore loss. Increased browsing pressure at uniform intensity across the landscape changes the selective environment of the vegetation. Plant communities shift from a diverse community to one dominated by a few taxa that can tolerate herbivory. Large carnivore loss has occurred at a global scale, creating similar habitats around the world and contributing to the global loss of biodiversity.

References

Altendorf, K.B., Laundré, J.W., López González, C.A., Brown, J.S. 2001. Assessing effects of predation risk on foraging behavior of mule deer. Journal of Mammalogy. 82(2): 430-439.

Arnqvist, G., Wooster, D. 1995. Meta-analysis: synthesizing research findings in ecology and evolution. Trends in Ecology and Evolution. 10(6): 236-240.

Ballard, W.B., Whitman, J.S., Gardner, C.L. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs. 98: 1-54.

Berger, J. 2005. Hunting by carnivores and humans: does functional redundancy occur and does it matter? In Ray, J.C., Redford, K.H., Steneck, R.S., Berger, J., editors. Large Carnivores and the Conservation of Biodiversity. Island Press, Washington, DC. 315-341.

Berger, J., Stacey, P.B., Bellis, L., Johnson, M.P. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications. 11(4): 947-960.

Beschta, R.L. 2003. Cottonwoods, elk, and wolves in the Lamar Valley of Yellowstone National Park. Ecological Applications. 13(5): 1295-1309.

Beschta, R.L. 2005. Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's northern range. Ecology. 86(2): 391-403.

Beschta, R.L., Ripple, W.J. 2007a. Increased willow heights along northern Yellowstone's Blacktail Deer Creek following wolf reintroduction. Western North American Naturalist. 67(4): 613-617.

Beschta, R.L., Ripple, W.J. 2007b. Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. Canadian Journal of Forest Research. 37: 1873-1885.

Beschta, R.L., Ripple, W.J. 2008. Wolves, trophic cascades, and rivers in the Olympic National Park, USA. Ecohydrology. 1(2): 118-130.

Beyer, H.L., Merrill, E.H., Varley, N., Boyce, M.S. 2007. Willow on Yellowstone's northern range: evidence for a trophic cascade? Ecological Applications. 17(6): 1563-1571.

Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology. 22(1): 37-47.

Brown, J.S., Arel, Y., Abramsky, Z., Kotler, B.P. 1992a. Patch use by gerbils (*Gerbillus allenbyi*) in sandy and rocky habitats. Journal of Mammalogy. 73(4): 821-829.

Brown, J.S., Morgan, R.A., Dow, B.D. 1992b. Patch use under predation risk: II. A test with fox squirrels, *Sciurus niger*. Annales Zoologici Fennici. 29(4): 311-318.

Brown, J.S., Laundré, J.W., Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy. 80(2): 385-399.

Carpenter, S.R., Kitchell, J.F., Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. BioScience. 35(10): 634-639.

Charnov, E.L. 1976. Optimal foraging, marginal value theorem. Theoretical Population Biology. 9(2): 129-136.

Childress, M.J., Lung, M.A. 2003. Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? Animal Behaviour. 66: 389-398.

DelGiudice, G.D., McCaffery, K.R., Beyer, D.E., Jr., Nelson, M.E. 2009. Prey of wolves in the Great Lakes Region. In Wydeven, A.P., Van Deelen, T.R., Heske, E.J., editors. Recovery of Gray Wolves in the Great Lakes Region of the United States: An Endangered Species Success Story. Springer. 155-173.

Druce, D.J., Brown, J.S., Castley, J.G., Kerley, G.I.H., Kotler, B.P., Slotow, R., Knight, M.H. 2006. Scale-dependent foraging costs: habitat use by rock hyraxes (*Procavia capensis*) determined using giving-up densities. Oikos. 115(3): 513-525.

Estes, J.A., Palmisano, J.F. 1974. Sea otters: their role in structuring nearshore communities. Science. 185(4156): 1058-1060.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T., Mao, J.S. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology. 86(5): 1320-1330.

Gasaway, W.C., Boertje, R.D., Grangaard, D.V., Kelleyhouse, D.G., Stephenson, R.O., Larsen, D.G. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs. 120: 1-59.

Guerra, V., Vickery, W.L. 1998. How do red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, coexist? Oikos. 83(1): 139-144.

Hairston, N.G., Smith, F.E., Slobodkin, L.B. 1960. Community structure, population control, and competition. The American Naturalist. 94(879): 421-425.

Halofsky, J., Ripple, W. 2008. Linkages between wolf presence and aspen recruitment in the Gallatin elk winter range of southwestern Montana, USA. Forestry. 81(2): 195-207.

Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E., Paquet, P.C. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology. 86(8): 2135-2144.

Hedges, L.V., Vevea, J.L. 1998. Fixed- and random-effects models in meta-analysis. Psychological Methods. 3(4): 486-504.

Hedges, L.V., Gurevitch, J., Curtis, P.S. 1999. The meta-analysis of response ratios in experimental ecology. Ecology. 80(4): 1150-1156.

Herman, C.S., Valone, T.J. 2000. The effect of mammalian predator scent on the foraging behavior of *Dipodomys merriami*. Oikos. 91(1): 139-145.

Hochman, V., Kotler, B.P. 2006. Effects of food quality, diet preference and water on patch use by Nubian ibex. Oikos. 112(3): 547-554.

Hochman, V., Kotler, B.P. 2007. Patch use, apprehenstion, and vigilance behavior of Nubian Ibex under perceived risk of predation. Behavioral Ecology. 18(2): 368-374.

Hunter, M.D., Price, P.W. 1992. Playing chutes and ladders: Heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology. 73(3): 724-732.

Hunter, L.T.B., Skinner, J.D. 1998. Vigilance behaviour in African ungulates: The role of predation pressure. Behaviour. 135(2): 195-211.

Jacob, J., Brown, J.S. 2000. Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. Oikos. 91(1): 131-138.

Kay, C.E. 2001. Long-term aspen exclosures in the Yellowstone ecosystem. USDA Forest Service Proceedings RMRS-P-18. Rocky Mountain Research Station, Fort Collins, CO.

Kotler, B.P. 1997. Patch use by gerbils in a risky environment: manipulating food and safety to test four models. Oikos. 78(2): 274-282.

Kotler, B.P., Dickman, C.R., Brown, J.S. 1998. The effects of water on patch use by two Simpson Desert granivores (*Corvus coronoides* and *Pseudomys hermannsburgensis*). Australian Journal of Ecology. 23(6): 574-578.

Kotler, B.P., Brown, J.S., Bouskila, A. 2004. Apprehension and time allocation in gerbils: the effects of predatory risk and energetic state. Ecology. 85(4): 917-922.

Laundré, J.W., Hernández, L., Altendorf, K.B. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology. 79(8): 1401-1409.

Leopold, A., Sowls, L.K., Spencer, D.L. 1947. A survey of over-populated deer ranges in the United States. Journal of Wildlife Management. 11(2): 162-177.

Lidicker, W.Z., Jr., Stenseth, N.C. 1992. To disperse or not to disperse: who does it and why?. In Stenseth, N.C., Lidicker, W.Z., Jr., editors. Animal Dispersal: Small Mammals as a Model. Chapman and Hall, London, UK. 21-36.

Lima, S.L., Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology. 68(4): 619-640.

Mao, J.S., Boyce, M.S., Smith, D.W., Singer, F.J., Vales, D.J., Vore, J.M., Merrill, E.H. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. Journal of Wildlife Management. 69(4): 1691-1707.

Martin, P.S. 1973. The discovery of America. Science. 179(4077): 969-974.

McKinney, M.L., Lockwood, J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution. 14(11): 450-453.

McLaren, B.E., Peterson, R.O. 1994. Wolves, moose, and tree rings on Isle Royale. Science. 266(5190): 1555-1558.

Mech, L.D., Karns, P.D. 1977. Role of the wolf in a deer decline in the Superior National Forest. USDA Forest Service Research Report NC-148. North Central Forest Experiment Station, St. Paul, MN.

Messier, F., Crete, M. 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia. 65(4): 503-512.

Microsoft Office. 2007. Microsoft for Windows. Excel.

Milchunas, D.G., Noy-Meir, I. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. Oikos. 99(1): 113-130.

Mohr, K., Vibe-Petersen, S., Lau Jeppesen, L., Bildsøe, M., Leirs, H. 2003. Foraging of multimammate mice, *Mastomys natalensis*, under different predation pressure: cover, patch-dependent decisions and density-dependent GUDs. Oikos. 100(3): 459-468.

Nelson, M.E., Mech, L.D. 2006. A 3-decade dearth of deer (*Odocoileus virginianus*) in a wolf (*Canis lupus*)-dominated ecosystem. American Midland Naturalist. 155(2): 373-382.

Oksanen, L., Fretwell, S.D., Arruda, J., Niemela, P. 1981. Exploitation ecosystems in gradients of primary productivity. The American Naturalist. 118(2): 240-261.

Olden, J.D., Rooney, T.P. 2006. On defining and quantifying biotic homogenization. Global Ecology and Biogeography. 15(2): 113-120.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution. 14(12): 483-488.

Paine, R.T. 1966. Food web complexity and species diversity. The American Naturalist. 100(910): 65-75.

Paine, R.T. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology. 49(3): 667-685.

Pickett, K.N., Hik, D.S., Newsome, A.E., Pech, R.P. 2005. The influence of predation risk on foraging behaviour of brushtail possums in Australian woodlands. Wildlife Research. 32(2): 121-130.

Polis, G.A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos. 86(1): 3-15.

Polis, G.A., Strong, D.R. 1996. Food web complexity and community dynamics. The American Naturalist. 147(5): 813-846.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T. 1996. Challenges in the quest for keystones. BioScience. 46(8): 609-620.

Pusenius, J., Schmidt, K.A. 2002. The effects of habitat manipulation on population distribution and foraging behavior in meadow voles. Oikos. 98(2): 251-262.

Ripple, W.J., Larsen, E.J. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biological Conservation. 95(3): 361-370.

Ripple, W.J., Beschta, R.L. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience. 54(8): 755-766.

Ripple, W.J., Beschta, R.L. 2006. Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. Biological Conservation. 133(4): 397-408.

Ripple, W.J., Beschta, R.L. 2007. Hardwood tree decline following large carnivore loss on the Great Plains, USA. Frontiers in Ecology and the Environment. 5(5): 241-246.

Ripple, W.J., Beschta, R.L. 2008. Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. Biological Conservation. 141(5): 1249-1256.

Ripple, W.J., Rooney, T.P., Beschta, R.L. In press. Large predators, deer, and trophic cascades in boreal and temperate ecosystems. In Terborgh, J., Estes, J.A., editors. The Science of Trophic Cascades. Island Press, Washington, DC.

Rooney, T.P. 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecology. 202(1): 103-111.

Rooney, T.P., Dress, W.J. 1997. Species loss over sixty-six years in the ground-layer vegetation of Heart's Content, an old-growth forest in Pennsylvania, USA. Natural Areas Journal. 17(4): 297-305.

Rooney, T.P., Waller, D.M. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management. 181(1-2): 165-176.

Rooney, T.P., Wiegmann, S.M., Rogers, D.A., Waller, D.M. 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. Conservation Biology. 18(3): 787-798.

Schmidt, K.A. 2000. Interactions between food chemistry and predation risk in fox squirrels. Ecology. 81(8): 2077-2085.

Schmitz, O.J., Hambäck, P.A., Beckerman, A.P. 2000. Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. The American Naturalist. 155(2): 141-153.

Schmitz, O.J., Krivan, V., Ovadia, O. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecology Letters. 7(2): 153-163.

Silva, W.P. 2008. xyExtract Graph Digitizer. v4.1.

Smith, W.P. 1991. *Odocoileus virginianus*. Mammalian Species. 388: 1-13.

Smith, D.W., Peterson, R.O., Houston, D.B. 2003. Yellowstone after wolves. BioScience. 53(4): 330-340.

Terborgh, J., Lopez, L., Nuñez, P., V., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D., Balbas, L. 2001. Ecological meltdown in predator-free forest fragments. Science. 294(5548): 1923-1926.

Terborgh, J., Holt, R.D., Estes, J.A. In press. Trophic cascades: What they are, how they work, and why they matter. In Terborgh, J., Estes, J.A., editors. The Science of Trophic Cascades. Island Press, Washington, DC.

Thiemann, J.A., Webster, C.R., Jenkins, M.A., Hurley, P.M., Rock, J.H., White, P.S. 2009. Herbaceous-layer impoverishment in a post-agricultural southern Appalachian landscape. American Midland Naturalist. 162(1): 148-168.

Tuen, A.A., Brown, J.S. 1996. Evaluating habitat suitability for tree squirrels in a suburban environment. Malaysian Applied Biology. 25(2): 1-8.

Verdolin, J.L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial ecosystems. Behavioral Ecology and Sociobiology. 60(4): 457-464.

Webster, C.R., Rock, J.H., Froese, R.E., Jenkins, M.A. 2008. Drought-herbivory interaction disrupts competitive displacement of native plants by *Microstegium vimineum*, 10-year results. Oecologia. 157(3): 497-508.

Werner, E.E., Peacor, S.D. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology. 84(5): 1083-1100.

White, C.A., Feller, M.C., Bayley, S. 2003. Predation risk and the functional response of elk-aspen herbivory. Forest Ecology and Management. 181(1-2): 77-97.

Winnie, J., Jr., Creel, S. 2007. Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. Animal Behaviour. 73: 215-225.

Wolf, E.C., Cooper, D.J., Hobbs, N.T. 2007. Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. Ecological Applications. 17(6): 1572-1587.

Wolff, J.O., Van Horn, T. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. Canadian Journal of Zoology. 81(2): 266-271.

Yunger, J.A., Meserve, P.L., Gutiérrez, J.R. 2002. Small-mammal foraging behavior: mechanisms for coexistence and implication for population dynamics. Ecological Monographs. 72(4): 561-577.